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ABSTRACT

A model was constructed to simulate the dynamics of a commercially harvested alligator (*Alligator mississippiensis* Daudin) population inhabiting the privately owned coastal marshland of Cameron and Vermilion parishes, Louisiana. In the model, nesting effort, nest flooding, desiccation mortality, and predation on alligator eggs and young were all determined as functions of monthly water depth averages. Cannibalism was considered to be the major density dependent factor operating on the population and was determined as a function of total population density and marsh water depth. The model contained a freeze mortality which was based on minimum winter temperatures. In addition, the model included a harvest option which resulted in alligator hunting mortality.

Comparison of simulation results with 1970-1973 nest count results demonstrated reasonably close agreement between simulated and observed data. Simulations of a June drought, a severe summer drought, and an August hurricane produced drastic population declines, although rapid recoveries were made in subsequent years. Environmentally stochastic simulations produced extremely irregular population response curves and resultant age structures.

Simulations were utilized to examine population response to various differential harvest rates in which age and sex-specific proportions of animals taken were similar to those observed in the 1972 and 1973 Louisiana harvest seasons. These simulations demonstrated that under existing habitat conditions a base population of 100,000 animals should be maintained for at least 20 years when subjected to an annual differential harvest rate slightly greater than 5 percent. Simulations were conducted using proportional harvest rates in which animals of various sizes were taken in proportion to their relative abundance in the population. Comparison of proportional and differential harvest strategies indicated that proportional hunting can result in increased yields of alligator hide and resultant income. Simulations with egg collection management programs produced greater population increases than similar simulations with no management.

Simulation of a Commercially Harvested Alligator Population in Louisiana

James D. Nichols[1], Lynn Viehman[2], Robert H. Chabreck[3] and Bruce Fenderson[4]

INTRODUCTION

The American alligator is native to the southeastern portion of the United States and occurs in Louisiana, Florida, Georgia, South Carolina, Texas, Arkansas, Mississippi, Alabama, and North Carolina. Reports of early settlers and explorers in the southeastern part of the country emphasized the abundance of alligators, and in the early 19th century the reptile was apparently present in tremendous numbers (Chabreck 1967a).

Commercial harvesting of alligators began in the mid-19th century (Smith 1893), and peak harvests were realized in the late 1800's (McIlhenny 1935). Stevenson (1904) estimated that the alligator populations of Florida and Louisiana were reduced by 80 percent between 1880 and 1904. Heavy harvests continued, and by 1960 the alligator had been practically eliminated from most of its original range (Chabreck 1967a).

Despite a continuous decline in numbers since 1950, no significant effort was made to protect the alligator until the 1960's. During the 1960's, protective legislation was enacted by all states within the animal's range, and in 1966 the alligator was placed on the federal list of rare and endangered species. Then, in 1970, the United States Congress effected the Endangered Species Conservation Act and the amendment to the 1906 Lacey Act which prohibited interstate shipment of illegally taken alligators (Palmisano 1972). The combined effect of this federal action and the various state laws was sufficient to largely curtail illegal killing of alligators (Chabreck 1971a).

Alligator numbers in the southeastern United States have increased in recent years (Powell 1971), and this increase has been reported by workers in South Carolina (Bara 1971), Florida (Schemnitz 1972), and Louisiana (Palmisano 1972; Joanen and McNease 1972a, 1972b; Palmisano *et al.* 1973). The dramatic recovery of the American alligator has been noted by the IUCN Crocodile Specialists Group, which transferred the alligator from the "critically endangered" category to the "recovered"

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category in 1971 (Bustard 1971) and reaffirmed this assessment in 1973 (Crocodile Specialists Group 1973).

In 1958, the Louisiana Wildlife and Fisheries Commission initiated an intensive alligator research program, the results of which have been summarized by Chabreck (1971a), Joanen and McNease (1973a), and Palmisano *et al.* (1973). The commission also effected various management procedures which included strict harvest control, restocking, and increased law enforcement efforts against poaching. These management efforts resulted in dramatic increases in the alligator population, and, by the late 1960's, high alligator densities existed in the coastal marshes of southwestern Louisiana. In 1970, the Louisiana state legislature established the framework for an open alligator season, and in 1972 and 1973 experimental harvests were conducted in the marshland of Cameron and Vermilion parishes. Preliminary results indicate that the 1972 harvest had no detrimental effect on the Cameron Parish alligator population (Palmisano *et al.* 1973).

Experimental harvest manipulations involving wild populations are potentially more dangerous to alligators than to most other commercially important wildlife species. This potential danger results from the high vulnerability of alligators to hunting, the long period required by alligators to reach sexual maturity, and the drastic effects of such natural phenomena as drought, severe freezes, and hurricanes on alligator populations.

The present study involves the use of computer simulation as a means of examining consequences of various alligator management strategies. The first objective of this study was to assemble all available information on the natural history and population dynamics of alligators and to use this information to construct a simulation model. The second major objective involved using the simulation model to examine the consequences of various alligator management strategies. The study's third objective was to examine possible long-term effects of different environmental changes on alligator populations. It was hoped that information provided by the study would not only be valuable in the management of the American alligator but would also serve as a basis for planning management strategies for other crocodilians throughout the world.

DESCRIPTION OF STUDY AREA

The model was constructed to simulate the alligator population inhabiting the privately owned marshland of Cameron and Vermilion parishes, Louisiana. This area comprises 1,144,600 acres of marsh (Joanen and McNease 1973b), and includes the land on which both Louisiana alligator harvests were conducted. The 1972 Louisiana alligator harvest was restricted to 278,168 acres of Cameron Parish marshland (Joanen *et al.* 1972, Palmisano *et al.* 1973), and the 1973 harvest was conducted on 541,361 acres in Cameron and Vermilion parishes (Joanen *et al.* 1973).

The Louisiana coastal region has been divided into three physiographic zones: the chenier plain, the sub-delta, and the active delta (O'Neil 1949). The study area was located in the chenier plain marsh zone of southwestern Louisiana, which contained the largest alligator population of the three zones. The chenier plain marsh zone borders the Gulf of Mexico, extends inland approximately 32 km (20 miles), and consists of coastal marshland interlaced with a network of bayous, canals, and lakes. The surface is relatively flat, and elevations average only about 30 cm (1 foot) above mean sea level (MSL); consequently, drainage in the area is quite slow. The only relief features are spoil deposits along canals and stranded beach ridges, locally called cheniers.

The Louisiana coastal marshes have been subdivided into four primary vegetative types: fresh, intermediate, brackish, and saline (Penfound and Hathaway 1938, Chabreck 1972). The study area included fresh, intermediate, and brackish marsh types, and recent descriptions of these types have been provided by Chabreck (1972). The fresh marsh was preferred by nesting female alligators to the other marsh types (Joanen and McNease 1972a).

Water depth in relation to the marsh elevation appeared to be an environmental parameter of extreme importance to alligators, and 9 years of water level data were obtained for the months April through October from stations within the study area (Table 1). Extreme fluctuations in water levels are associated with periods of prolonged drought with levels declining to as much as 61 cm (2 feet) below the marsh surface (Nichols 1959) or hurricanes with water inundating the marsh to a depth of 91 to 274 cm (3 to 9 feet). In the construction of various water level functions in the model, 15 cm (.5 foot) was generally considered to be the mean annual marsh water depth value (Chabreck 1960).

Data on water levels and alligator sizes in the United States are often expressed in linear foot measurements; consequently, the measure-

Table 1.—Marsh water depths in the study area[a]

Year	April	May	June	July	August	September	October
				cm (feet)			
1965	12 (.4)	21 (.7)	18 (.6)	0 (.0)	6 (.2)	18 (.6)	24 (.8)
1966	12 (.4)	49 (1.6)	27 (.9)	24 (.8)	34 (1.1)	55 (1.8)	58 (1.9)
1967	21 (.7)	46 (1.5)	27 (.9)	15 (.5)	24 (.8)	49 (1.6)	27 (.9)
1968	24 (.8)	18 (.6)	12 (.4)	21 (.7)	27 (.9)	27 (.9)	21 (.7)
1969	18 (.6)	46 (1.5)	27 (.9)	3 (.1)	15 (.5)	24 (.8)	18 (.6)
1970	30 (1.0)	27 (.9)	37 (1.2)	24 (.8)	21 (.7)	34 (1.1)	40 (1.3)
1971	18 (.6)	3 (.1)	12 (.4)	0 (.0)	37 (1.2)	24 (.8)	43 (1.4)
1972	9 (.3)	24 (.8)	18 (.6)	9 (.3)	21 (.7)	15 (.5)	40 (1.3)
1973	18 (.6)	24 (.8)	27 (.9)	24 (.8)	37 (1.2)	24 (.8)	40 (1.3)
Mean	18 (.6)	27 (.9)	24 (.8)	12 (.4)	24 (.8)	30 (1.0)	34 (1.1)
St. Dev.	5.2 (.17)	13.4 (.44)	8.5 (.28)	8.8 (.29)	8.5 (.28)	11.9 (.39)	11.0 (.36)

[a]Source: Chabreck and Joanen (1966, 1967); Joanen *et al.* (1968, 1969, 1970, 1971, 1972, 1973, 1974).

ments presented in this report are expressed in the same manner to facilitate the interpretation of data. A metric conversion is also presented to comply with international standards.

ALLIGATOR POPULATION BIOLOGY

Size-Age Relationship

In most of the alligator literature, animals are categorized on the basis of total body length and are separated into one-foot size classes. The present study required age-specific rather than size-specific data, however, and information on alligator growth rates was necessary for such data conversions.

Alligator growth rate data have been presented by Reese (1915), Neill (1971), Chabreck (1965), Hines *et al.* (1968), and McIlhenny (1934), and the latter three reports seem to provide the best information for wild alligators. Chabreck (1965) presented average sizes of 1- and 2-year-old alligators in Louisiana. Hines *et al.* (1968) found a growth rate of 2.95 cm (1.16 inches) per month for immature alligators in the Florida Everglades. The Everglades growth data are not applicable to Louisiana alligators, however, because the Louisiana animals enter a semidormant stage during cold weather (McIlhenny 1935, Chabreck 1965) while Everglades animals do not become semidormant (Thompson and Gidden 1972). This difference in winter activity between Everglades and Louisiana alligators probably results in a higher growth rate for Everglades animals.

McIlhenny (1934) toe-marked and released 38 alligator hatchlings on Avery Island, Louisiana, and followed their growth for 11 years. Visual fit curves were derived from McIlhenny's data and these curves were projected beyond the last data points through 21 years (Figure 1). Perhaps it should be noted that these curves are not actually continuous throughout each year as the graph might indicate. Instead, alligator growth slows during the winter months and increases during the spring, summer, and fall. The curves were used to establish a general size-age relationship table which applies to alligators in the late summer of the specified years (Table 2). Table 2 was used in all conversions of size-specific to age-specific data. It should be emphasized that although McIlhenny's (1934) data are considered adequate for the model, additional research on alligator growth rates is certainly needed.

Food intake and temperature are variables which can affect alligator growth rate (Coulson *et al.* 1973), but no accurate data regarding these relationships are available for wild populations. McIlhenny's (1934) data were obtained in the coastal marshland of southwestern Louisiana, and it was assumed that the general temperature regime and the types of alligator prey species available were much the same as those existing on the study area. Regarding food availability, alligators utilize a wide variety of food sources, and it is difficult to imagine that they would be

subjected to food shortages as frequently as other more specialized predator species. Chabreck (1971b) found that alligators exposed to saline conditions consumed less food than animals inhabiting fresh water areas. The study area for the simulated population, however, included virtually no saline areas, and this variable was thus ignored.

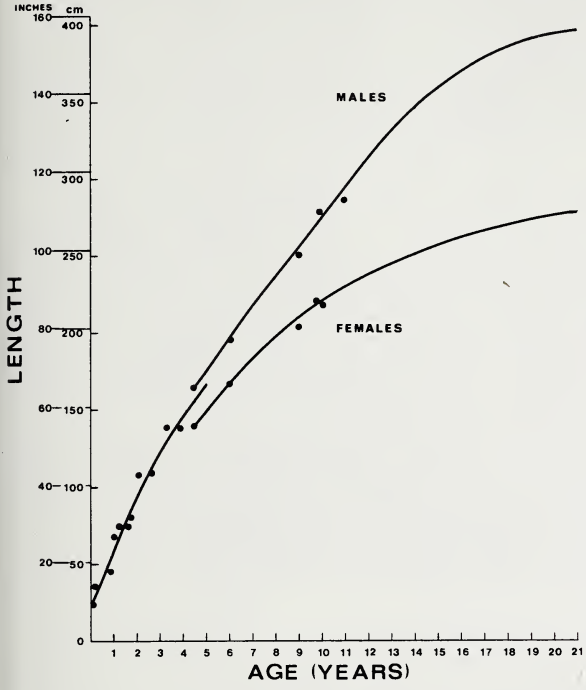

Figure 1.—Relationship between total length and age in alligators. Years begin September 1 and end August 31.

Table 2.—Alligator size-age relationship[a]

Age (years)	Body length[b]		Age (years)	Body length[b]	
	Males	Females		Males	Females
	— — — Meters (feet) — — —			— — — Meters (feet) — — —	
1	.3- .6 (1-2)	.3- .6 (1-2)	12	2.7-3.0 (9-10)	2.1-2.4 (7-8)
2	.6- .9 (2-3)	.6- .9 (2-3)	13	3.0-3.4 (10-11)	2.1-2.4 (7-8)
3	.9-1.2 (3-4)	.9-1.2 (3-4)	14	3.0-3.4 (10-11)	2.1-2.4 (7-8)
4	1.2-1.5 (4-5)	1.2-1.5 (4-5)	15	3.4-3.7 (11-12)	2.4-2.7 (8-9)
5	1.5-1.8 (5-6)	1.2-1.5 (4-5)	16	3.4-3.7 (11-12)	2.4-2.7 (8-9)
6	1.5-1.8 (5-6)	1.5-1.8 (5-6)	17	3.7-4.0 (12-13)	2.4-2.7 (8-9)
7	1.8-2.1 (6-7)	1.5-1.8 (5-6)	18	3.7-4.0 (12-13)	2.4-2.7 (8-9)
8	2.1-2.4 (7-8)	1.5-1.8 (5-6)	19	3.7-4.0 (12-13)	2.4-2.7 (8-9)
9	2.4-2.7 (8-9)	1.8-2.1 (6-7)	20	3.7-4.0 (12-13)	2.4-2.7 (8-9)
10	2.4-2.7 (8-9)	1.8-2.1 (6-7)	21	3.7-4.0 (12-13)	2.4-2.7 (8-9)
11	2.7-3.0 (9-10)	1.8-2.1 (6-7)			

[a]Basically derived from McIlhenny (1934).

[b]Sizes generally apply to alligators at the beginning (September) of the designated year class.

Reproductive Biology

Alligator Courtship and Nesting—General Information

Alligator courtship and breeding were found to occur between May 18 and May 31 in a recent study in southwestern Louisiana (Joanen and McNease 1970a). Courtship activity during this time is apparently restricted to open water areas including bayous and canals, and marsh lakes and ponds greater than one acre in size (Joanen and McNease, 1970a). After courtship the adult females travel to dens in the interior marsh to construct nests and lay eggs. Details of alligator nest construction have been provided by Reese (1907), Kellogg (1929), Arthur (1931), McIlhenny (1934), Bellairs (1969), Joanen (1969), and Neill (1971).

In a 5-year study in southwestern Louisiana, Joanen (1969) found that the peak alligator nesting period varied between June 15 and June 28. Joanen correlated these peak nesting periods with average March, April, and May temperatures, but because he found only a 13-day difference between dates of peak nesting activity, the temperature-nesting period relationship was ignored in the model. Instead, nesting was assumed to occur at the end of June in each year.

Joanen (1969) reported that the number of eggs per nest ranged from 2 to 58 during his 5-year study. The average number of eggs per nest was 38.9, and this figure was incorporated in the model as a constant. The incubation period for alligator eggs is approximately 63 to 65 days (Chabreck 1967b, Joanen 1969). In the model, hatching thus occurred at the end of August.

Age of Sexual Maturity

Virtually all authorities agree that the female alligator reaches maturity at 1.8 meters (6 feet). In a sample of female alligators examined internally on Sabine National Wildlife Refuge in Louisiana, Giles and Childs (1949) found only one breeding female under 1.8 meters (6 feet) in length, and even this animal was believed to have approached this size. In his Rockefeller Refuge study, Joanen (1969) found that sizes of nesting females varied between 1.8 and 2.6 meters (6 and 8.5 feet). Kleibert (pers. comm.) has indicated that females generally begin nesting at age 9, and this corresponds to the beginning of the year at which female alligators move to the 1.8 to 2.1 meter (6 to 7 feet) size class (Table 2). In the model, female alligators were assumed to become sexually mature at age 9 and to continue breeding throughout the remainder of their lives.

All 1.8-4.0 meter (6-13 feet) male alligators examined by Joanen and McNease (1973a) were found to be physiologically capable of reproduction. Because of the usual surplus of males in adult alligator populations (Chabreck 1966) and because of the ability of individual males to breed with more than one female per season (Chabreck 1965),

the number of adult males was considered to be unimportant in the computation of nesting females.

Nesting Effort

Chabreck (1966) cited data from Sabine Refuge kill survey records indicating that 68.1 percent of a sample of 69 adult females nested during one year. More recent work in southwestern Louisiana has indicated that 67 percent of the adult female segment of an alligator population is capable of reproducing during any given year (Joanen and McNease 1973a).

In 1971, alligator nest counts in southwestern Louisiana indicated that nesting had decreased by 39.5 percent from the previous year (Joanen and McNease 1972c). Joanen and McNease felt that the decreased number of nests was due to dry nesting conditions rather than to a decrease in the mature female segment of the population. These workers further stated that "nesting success may be proportional to the amount of surface water accrued during the spring on until actual egg deposition" (Joanen and McNease 1972c). This 1971 nesting decline has also been attributed to dry nesting conditions in later reports (Joanen and McNease 1973b, Palmisano *et al.* 1973), and Schemnitz (1972) has cited low water levels as the reason for a 1971 decline in alligator nesting in the Florida Everglades. Joanen and McNease (1970a, 1972a) stressed the need of female alligators for open water during courtship, and it is possible that this is part of the mechanism explaining reduced nesting effort during drought.

The nesting effort-water depth relationship appears to be extremely important to alligator population growth, and the relationship was thus included in the model. Using 1970 nest count data as a base, Joanen and McNease (1972c) reported percent changes in numbers of nests counted in 1971 for the three major Louisiana marsh zones, the chenier plain, −39.5 percent; the sub-delta, −6.0 percent; and the active delta, −22.1 percent. The chenier plain and sub-delta zones had much higher alligator populations than did the active delta, and nesting changes in these two zones were thus used to determine the nesting effort-water depth relationship.

Joanen and McNease (1972c) compared average January to June rainfall with alligator nesting success and noted the importance of the total surface water available during the spring. May and June marsh water depths are apparently important in regard to nesting effort, and this relationship was used in the model.

Chenier plain May-June water depth averages for the years 1970-1973 (Table 1) were plotted against total January to June rainfall (Figure 2). This relationship was assumed to be linear, and a visual fit line was drawn. Points corresponding to sub-delta rainfall figures were then marked along this line, and the average May-June water depth values were obtained from these points. This plot requires the assumption that

rainfall and marsh water depth are similarly related in the chenier plain and sub-delta marsh zones. This assumption has not been tested, but drainage patterns in the two zones are similar, and the relationships should be basically the same.

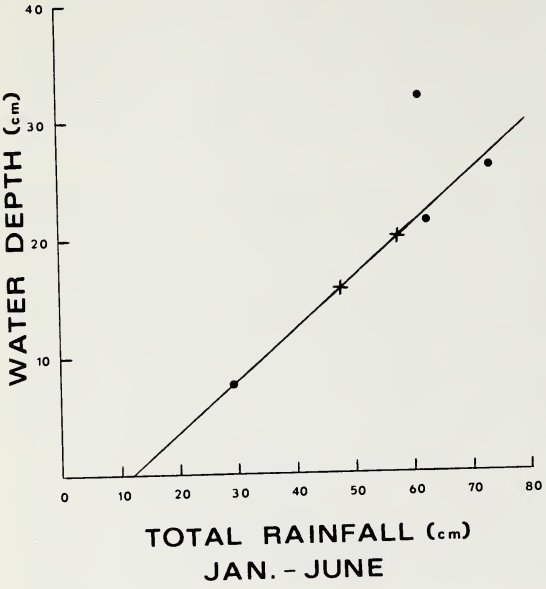

Figure 2.—Relationship between May-June marsh water depth averages and total January to June rainfall. Data points used in the construction of this relationship correspond to chenier plain water depths and rainfall levels, 1970-1973. Points denoted x were obtained by plotting sub-delta marsh rainfall figures and were used to project sub-delta water depth estimates.

Joanen and McNease (1972c, 1973b) and Palmisano *et al.* (1973) used 1970 nest count data as a basis for comparison with subsequent (1971-1973) nest counts and population estimates. The 1970 alligator population estimate was computed using a 67 percent value for nesting effort, and the assumption is thus implied that 67 percent of the adult females nested in 1970. Using 67 as the percentage of females nesting in 1970, and using the figures for percent decrease in nesting females supplied by Joanen and McNease (1972c) for the sub-delta and chenier plain marsh zones, values were computed for the percentages of mature females nesting in 1971 (Table 3).

Table 3.—Computed nesting effort as related to marsh water depths during May and June

Marsh zone	Year	Water depth [cm (feet)]	Percent mature females nesting
Chenier Plain	1970	32 (1.05)[a]	67.0
Sub-Delta	1970	20 (.65)[b]	67.0
Chenier Plain	1971	8 (.25)[a]	40.5[c]
Sub-Delta	1971	15 (.50)[b]	63.0[c]

[a]From Joanen *et al.* (1971).

[b]Derived from Figure 2 and rounded to the nearest 1.5 cm.

[c]Computed from percent changes in nesting success reported by Joanen and McNease (1972c).

The minimum value for percent nesting effort was rather arbitrarily assumed to be 33.5, or a 50 percent decrease from years of normal water level. Joanen and McNease (1972c) noted one nesting success change of −80 percent, but the area sampled was very small and the value was thus not used. It was further assumed that minimum nesting occurred at the marsh water depth of 0 cm, and this assumption should certainly be studied further. The minimum water depth at which 67 percent nesting effort occurs was set at 20 cm (.65 foot), as shown in Table 3. These data points were plotted and a curve was visually fit (Figure 3). In the model, the percentage of mature females nesting was determined from the curve, and this percentage was then applied to the number of mature females in the population at the end of June for each year.

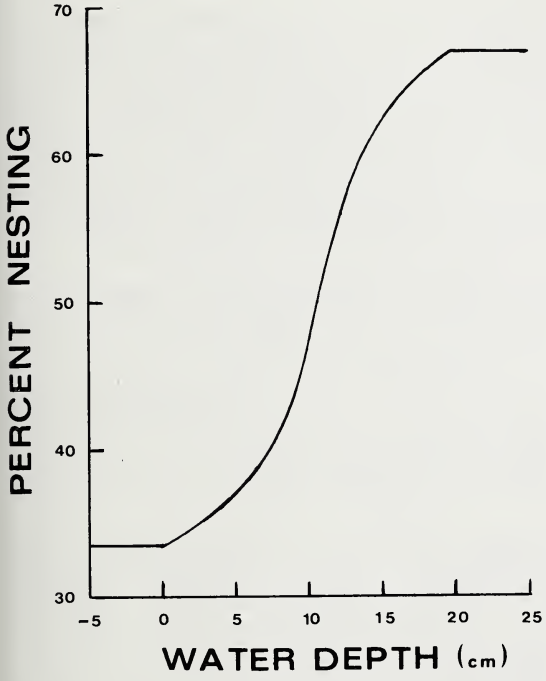

Figure 3.—Relationship between the percentage of mature female alligators nesting and marsh water depth (May-June average).

Nest Flooding

After nest construction and egg laying, alligator nests are vulnerable to flooding during times of high water. Flooding loss was reported to be a major source of egg mortality in the Florida Everglades (Hines *et al.* 1968) and can also cause considerable damage in Louisiana coastal marshland during certain years (Ensminger and Nichols 1957, Chabreck 1965).

The nest flooding-water depth relationship was obtained using data points from a variety of sources. In the model, the percentage of nests

lost to flooding was determined as a function of the highest monthly water depth average of the three months June, July, and August. These are the three months during which eggs usually incubate. Joanen (1969) reported mean egg cavity measurements for alligator nests, and these data were used to obtain the maximum water depth at which no nest flooding would occur. Joanen's measurements indicate that a standing water depth of 26 cm (.85 foot) would reach the bottom of the first layer of eggs in the average nest. It was assumed that the average nest would lose some eggs to flooding at 27 cm (.9 foot). An arbitrary figure, 3 cm (.1 foot), was then subtracted from 27 cm (.9 foot), to partially account for nests which contained deeper egg cavities than average nests. The maximum value at which no eggs are lost to flooding was thus set at 24 cm (.8 foot).

Another data point was chosen using the 2.1 percent average nest flooding figure reported by Joanen (1969). June, July, and August water depths for the years of Joanen's study are shown in Table 1. Marsh water depths for three of these months averaged 27 cm (.9 foot), while the water depth for August 1966 averaged 34 cm (1.1 feet). The 2.1 percent flooding value represents six of Joanen's nests, and it was assumed that five of these nests were lost during the single month, August 1966. The five nests constituted approximately 8 percent of the nests followed during 1966.

Flemming (1974) followed 20 nests in the marsh and reported that 50 percent of these were flooded with a water depth of 37 cm (1.2 feet). Flemming's data apply only to marsh nests, and Joanen (1969) reported that 6.7 percent of the nests he observed were found on levees, above normal flood levels. Flemming's (1974) 50 percent figure was multiplied by Joanen's 93.3 percent marsh nesting figure, and it was calculated that 46.7 percent of all nests would be inundated with a water depth of 37 cm (1.2 feet).

Again using Joanen's (1969) egg cavity nest measurements, it was determined that all average marsh nests would be completely inundated with a water depth of 43 cm (1.4 feet). An additional 3 cm (.1 foot) was added to this value to include nests with relatively high egg cavities. It was thus calculated that a water depth of 46 cm (1.5 feet) would inundate all marsh nests, or 93.3 percent of the total nests. This figure is supported by data of Hines *et al.* (1968), who observed a 100 percent flooding loss of marsh nests with water depths of 55 cm (1.8 feet) and 70 cm (2.3 feet) in the Florida Everglades. Finally, it was assumed that all nests, including those built on levees, would be lost with water depths of 122 cm (4 feet) and greater. This 122 cm (4 feet) value is perhaps low and was simply intended to represent high marsh water levels associated with a hurricane. The various data points were plotted and lines were drawn to indicate a general nest flooding-water depth relationship (Figure 4). These baseline data can obviously be improved with further research efforts.

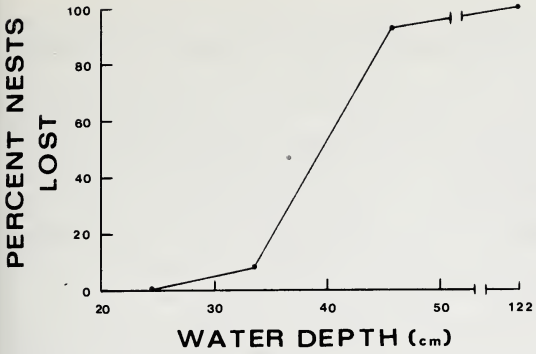

Figure 4.—Relationship between percent nest flooding and marsh water depth.

Levee Nesting

Levee nests apparently have different probabilities of being flooded and destroyed by predators than marsh nests, and it was thus important to investigate possible variability in the percentage of animals nesting on levees. Giles and Childs (1949) noted that adult females tended to use margins of ridges as nesting sites when marsh water levels were abnormally high. Ensminger and Nichols (1957) also reported increased nesting on levees in a year of high marsh water levels. However, Chabreck (1965) noted no relationship between nest location and water depth. Nesting alligators are very territorial and tend to nest in the same vicinity each year (Joanen 1969, Joanen and McNease 1970a). Joanen's (1969) 6.7 percent figure for levee nests was thus assumed to remain constant.

Nest Predation

Nest predation can be an important source of egg mortality. Joanen (1969) followed 266 nests during a 4-year period and reported that 16.5 percent of these nests were destroyed by raccoons, *Procyon lotor*. Joanen (1969) found that 50 percent of the levee nests he followed were taken by raccoons. Palmisano (pers. comm.) observed that 18-20 percent of all marsh nests are generally destroyed by raccoons, while approximately 50 percent of levee nests are destroyed.

Hines *et al.* (1968) reported the loss of one levee nest to a hog, *Sus scrofa*. Hogs are present in very low numbers in the southwestern Louisiana coastal marshes, and the number of alligator nests lost to them is insignificant. Kellogg (1929) reported finding three alligator eggs in the stomach of an alligator taken at Morgan City, Louisiana. Joanen (pers. comm.) noted that the stomach of a barren adult female alligator taken during the 1973 hunting season contained alligator eggs. These were isolated cases, however, and it is doubted that alligators are important nest predators.

The raccoon is by far the most important alligator nest predator, and it was the only predator considered in the model. Joanen (1969) found that nest predation by raccoons occurred just after the eggs began to

crack along the longitudinal axis, usually after seven weeks of incubation. Joanen also noted that after locating a nest, raccoons would generally return every few days for three or four visits until all eggs had been eaten. A raccoon which located a nest after 49 days of incubation and periodically returned to the nest every few days, would probably finish with the nest at approximately the time of hatching. Therefore, it is unlikely that a raccoon would ever prey upon more than one nest per year, and certainly never more than two. Because of this temporal limitation of nest availability, it was hypothesized that the predation rate would not increase as a function of alligator nest density.

Raccoon density must certainly affect the rate of nest predation, but unfortunately this relationship could not be incorporated into the model. Raccoon density in the Louisiana coastal marsh varies from approximately one raccoon per 5 acres to one per 10 acres (Palmisano, pers. comm.). Unfortunately, raccoon density data were not available for years in which raccoon predation rates on alligator nests were known.

Flemming (1974) felt that nest predation is possibly related to marsh water depth, with higher predation rates occurring in dry years. He believed that raccoon predation on nests is probably linked to food availability, and that more food is available to raccoons during wet years. Unpublished data on annual 1965-1968 predation rates were made available by Joanen (pers. comm.), and these rates were compared with August marsh water depths. Percent predation was plotted against August marsh water depths, and three points were taken directly from Joanen's (pers. comm.) data. The lowest observed nest predation rate was 1.7 percent, which was reported in 1965 when the August marsh water depth averaged 6 cm (.2 foot). This predation rate seemed extremely low, and the 1.7 percent value was arbitrarily doubled to obtain a minimum predation rate of 3.5 percent. Flemming (1974) observed no nest predation on 20 nests he followed in 1973. The August marsh water depth during that year was 37 cm (1.2 feet). Therefore, the minimum predation rate of 3.5 percent was set to correspond with this water depth.

These data points were plotted, and lines were drawn to indicate the nest predation-water depth relationship (Figure 5). The portion of the graph lying above 24 cm (.8 foot) follows the pattern predicted by Flem-

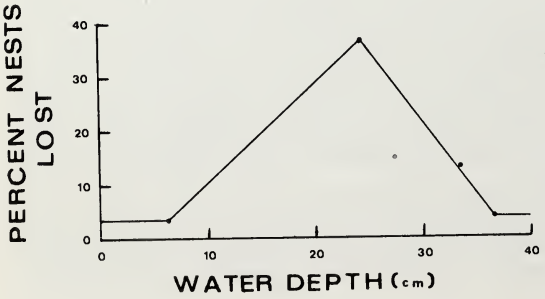

Figure 5.—Relationship between nest predation and marsh water depth.

ming (1974), with predation rate increasing as water level decreases. Below 24 cm (.8 foot), however, the relationship is contrary to what was expected.

If low predation rates do actually occur at low water levels, then such a relationship could be explained in several possible ways. The majority of alligator nests are built in the marsh interior, and perhaps during times of severe drought raccoons are less likely to leave large, permanent water sources and venture into the dry marsh in search of food. In times of drought, numerous raccoon prey species would probably be concentrated in any available bodies of water. Such a situation would eliminate the raccoon's need to venture into the interior marsh. Finally, most alligator nests are constructed near the female's hole or den, and females tend to remain near the den during periods of drought (Chabreck 1965). In a telemetric study of nesting females, Joanen and McNease (1970a) also noted that female movement was very restricted during the period of the year exhibiting the lowest water levels. By remaining in the proximity of the den and nest site during times of drought, females are probably better able to defend the nest against raccoons.

The relationship graphed in Figure 5 was used in the model, despite some doubts regarding the nature of the function. The inability to incorporate raccoon density into the model was unfortunate, and it is recommended that the raccoon density-nest predation relationship be studied in the future.

Hatching Success

Joanen (1969) found total hatching success to be 58.2 percent for 154 nests followed during 1967 and 1968. Joanen (1969) also reported a 4-year average predation and flooding loss value of 18.6 percent. This latter value was added to the total hatching success figure to obtain a survival rate for eggs which are not destroyed by nest predation and flooding. It was thus calculated that 76.8 percent of all eggs which survive predation and flooding hatch successfully. This value was incorporated into the model as a constant.

Alligator Population Structure and Mortality Relationships

Average Annual Mortality and Survival Rates

Before investigating alligator population structure and specific mortality functions, it was necessary to obtain average annual mortality rates for the different age classes in the alligator population. Alligator population dynamics have never been adequately studied, however, and no reliable mortality rate estimates could be found in the literature.

Chabreck (1966) presented night count results which indicated the size structure of the Rockefeller Refuge alligator population at the time of his study. This size structure could theoretically be used to construct a static or time-specific life table, and mortality rates could be obtained in this manner. Static life tables, however, require the assumptions that the environment does not change from year to year and that the population is at equilibrium (Krebs 1972), and neither of these assumptions could be met for the Rockefeller Refuge alligator population.

Harvest data were available for the 1972 and 1973 experimental seasons, and these data were manipulated to obtain one annual mortality estimate for 7-year-old males. This specific age and sex class was used because both 7- and 8-year-old males occupy single size classes, and mortality estimates for these animals are thus not confused by the existence of more than one age class per size category. The calculations invoked the assumption that 7-year-old males in 1972 and 8-year-old males in 1973 were harvested in proportion to their relative abundance in the sample population each year.

Two methods were used for taking alligators during the experimental harvest seasons, "fishing" with baited hook and line, and shooting. The fishing method was selective for larger animals (Palmisano *et al.* 1973), and it was decided to use only animals taken by this method in the calculations. The steps involved in the calculation of the 7-year-old male mortality rate are shown in Table 4. The final step involved subtracting the percent (25.30) mature male alligators caught by hook and line in the 1973, 2.1-2.4 meter (7-8 feet) size class, from the percent (32.11) mature male alligators caught by hook and line in the 1972, 1.8-2.1 meter (6-7 feet) size class. This difference of 6.81 percent was divided by 32.11 percent (again representing the 1.8-2.1 meter males in the 1972 sample) and a mortality rate of 21.2 percent was obtained.

After age 2, alligators are relatively free of most predation. Therefore, we assumed that mortality rates are the same for the alligator age classes 3-21, and the 21.2 percent annual mortality rate was considered to apply to all of these classes. After reaching maturity, female alligators move into the marsh interior, and their mortality rates probably decrease at this time (Chabreck 1965). Adult males, however, travel extensively (Joanen and McNease 1972b) and are subjected to a variety of hazards. Therefore, we assumed that adult males have twice the annual mortality rate of adult females.

The 21.2 percent annual mortality rate was broken down into seven equal monthly survival rates by solving for the equation $X^7 = (1-.212)$, and a .967 monthly survival rate was thus calculated. The .967 rate was applied to males and females aged 3 through 8 years. Assuming an adult sex ratio of 60.1 percent males (Chabreck 1966), differential annual survival rates were calculated to be .750 per year for males and .875 per year for females. The male mortality rate is therefore twice as high as the female rate. The annual survival rates reduce to .960 per month

Table 4.—Mortality rate calculations for seven-year-old males

Size class [meters (feet)]	Percent alligators caught by hook & line[a]	Percent alligators which were males[bc]	Percent alligators which were caught by hook & line which were males	Total number of alligators harvested[de]	Number of male alligators caught by hook & line	Percent mature male alligators caught by hook & line in each size class
	1972 Harvest					
1.8-2.1 (6-7)	75.00	82.43	61.82	327	202	32.11
2.1-2.4 (7-8)	79.17	70.00	55.42	288	160	25.44
2.4-2.7 (8-9)	79.31	93.55	74.19	149	111	17.65
2.7-3.0 (9-10)	96.67	100.00	96.67	93	90	14.31
3.0-3.4 (10-11)	88.24	100.00	88.24	57	50	7.95
3.4-3.7 (11-12)	66.67	100.00	66.67	16	11	1.75
3.7+ (12+)	100.00	100.00	100.00	5	5	0.79
	1973 Harvest					
1.8-2.1 (6-7)	75.00	47.06	35.30	724	256	23.38
2.1-2.4 (7-8)	79.17	62.11	49.17	564	277	25.30
2.4-2.7 (8-9)	79.31	77.27	61.28	323	198	18.08
2.7-3.0 (9-10)	96.67	97.14	93.91	176	165	15.07
3.0-3.4 (10-11)	88.24	100.00	88.24	139	123	11.23
3.4-3.7 (11-12)	66.67	100.00	66.67	90	60	5.48
3.7+ (12+)	100.00	100.00	100.00	16	16	1.46

[a]Source: Table 4 of Palmisano *et al.* (1973).
[b]Source (1972 data): Table 5 of Palmisano *et al.* (1973).
[c]Source (1973 data): McNease (pers. comm.).
[d]Source (1972 data): Table 3 of Palmisano *et al.* (1973).
[e]Source (1973 data): Table 1 of Joanen *et al.* (1973).

for males and .981 per month for females, and were applied to animals 9 through 21 years old.

Based on field observations of alligator populations, we estimated an average 65 percent mortality rate for 1-year-old animals and a 40 percent mortality rate for 2-year-olds. Both sexes are equally vulnerable at these ages, and average monthly survival rates were calculated to be .861 for 1-year-olds and .930 for 2-year-olds. Average annual and monthly survival rates are summarized in Table 5. As previously mentioned, all annual survival rates were broken down into seven monthly rates. It was assumed that all alligator mortality sources other than freezes occurred during the months April through October. The alligators were considered to be semidormant during the five months November through March, and few mortality sources probably operate during this period.

Table 5.—Average alligator survival rates

Age	Annual survival rate		Monthly survival rate	
	Male	Female	Male	Female
1	.350	.350	.861	.861
2	.600	.600	.930	.930
3	.788	.788	.967	.967
4	.788	.788	.967	.967
5	.788	.788	.967	.967
6	.788	.788	.967	.967
7	.788	.788	.967	.967
8	.788	.788	.967	.967
9	.750	.875	.960	.981
10	.750	.875	.960	.981
11	.750	.875	.960	.981
12	.750	.875	.960	.981
13	.750	.875	.960	.981
14	.750	.875	.960	.981
15	.750	.875	.960	.981
16	.750	.875	.960	.981
17	.750	.875	.960	.981
18	.750	.875	.960	.981
19	.750	.875	.960	.981
20	.750	.875	.960	.981
21	.750	.875	.960	.981

Population Age Structure

A general knowledge of the age structure of the alligator population was necessary before various mortality functions could be calculated. Chabreck (1966) presented results of night count surveys which indicated the size structure of the Rockefeller Refuge alligator population (Table 6). Chabreck believed his sample to be representative and combined his night count results with nest count data to estimate the total alligator population of Rockefeller Refuge.

Table 6.—The results of night counts and total population computation for alligators on Rockefeller Wildlife Refuge, 1966[a]

Total length size class [meters (feet)]	Number seen	Percentage composition	Total number on refuge
.3- .6 (1-2)	45	25.3	1,339
.6-.9 (2-3)	33	18.5	979
.9-1.2 (3-4)	30	16.8	888
1.2-1.5 (4-5)	24	13.5	714
1.5-1.8 (5-6)	18	10.1	534
1.8-2.1 (6-7)	13	7.3	386
2.1-2.4 (7-8)	8	4.5	238
2.4-2.7 (8-9)	4	2.3	122
2.7-3.0 (9-10)	2	1.1	58
3.0+ (10+)	1	.6	32
Total	178	100.0	5,291

[a]Source: Table 2 of Chabreck (1966).

Chabreck's (1966) night count data indicated the size structure of the alligator population at approximately the end of May and the beginning of June, 1966. Our calculations required a knowledge of September age structure, however, and because of the differential mortality rates operating on the population, the September size structure is expected to differ from the June size structure. It was, therefore, necessary to "back the population up" from June 1966 to September 1965. This was accomplished by dividing the number of animals comprising each size class,

Table 7.—Size-specific sex ratios used in the construction of alligator population structures[a]

Total body length	Males	Females
Meters (feet)	— — — — — — Percent — — — — — —	
.3- .6 (1-2)	60.1[b]	39.9
.6- .9 (2-3)	64.6	35.4
.9-1.2 (3-4)	62.8	37.2
1.2-1.5 (4-5)	53.5	46.5
1.5-1.8 (5-6)	52.4	47.6
1.8-2.1 (6-7)	64.1	35.9
2.1-2.4 (7-8)	60.1[c]	39.9
2.4-2.7 (8-9)	60.1[c]	39.9
2.7-3.0 (9-10)	60.1[c]	39.9
3.0-3.4 (10-11)	100.0	0.0
3.4-3.7 (11-12)	100.0	0.0
3.7+ (12+)	100.0	0.0

[a]Unless otherwise indicated, sex ratio data were obtained from 1,816 alligators captured alive in Louisiana from April 1959 to December 1966 (Chabreck unpubl. data).

[b]Average adult sex ratio (Chabreck 1966) was used because of inability to sex young alligators.

[c]Average adult sex ratio (Chabreck 1966) was used because of insufficient data (small sample sizes).

by the monthly size-specific survival rate taken to the fourth power (there are four months involved). For example, the number of .9-1.2 meter (3-4 feet) alligators in the June population was 888, so the number of .9-1.2 meter animals in the September population was equal to $888/(.967)^4 = 1{,}016$. These calculations yielded a new size structure characteristic of the beginning of September.

The September population size structure was then broken down by sex according to size-specific sex ratios (Table 7). These ratios were obtained from 1,816 alligators captured alive in Louisiana during the period 1959-1966. It is virtually impossible to accurately determine the sex of alligators less than .6 meter (2 feet) in length, and the average adult value of 60.1 percent males (Chabreck 1966) was thus used for these small animals. The 60.1 percent male value was also used for size classes in which the number of animals examined was insufficient.

Finally, it was necessary to determine the number of animals in each age class, within a given size and sex class. This was accomplished by assuming a stable age distribution within each size class and by solving the following equation for X:

$$\sum_{i=o}^{n} (Y)^i X = X + YX + (Y)^2 X + \ldots + (Y)^n X = Z$$

where n−1 equals the number of age classes in the given size class, Y equals the annual survival rate, Z equals the total number of animals in the size class, and X equals the number of animals in the youngest age class within the size class. The sizes of subsequent age classes within a size class were then obtained by multiplying the number of animals in the youngest age class by the appropriate power of the survival rate.

An example of the type of age structure derived from the calculations is presented in Table 8. This particular age structure was obtained starting with the June 1973 population estimate of 71,897 animals (Palmisano *et al.* 1973). The derived age structure contains 96,918 alligators and represents the September 1972 population.

Table 8.—Calculated age structure, September 1972

Age	Males	Females	Age	Males	Females
1	19,876	13,196	12	415	652
2	11,487	6,295	13	174	514
3	8,680	5,141	14	137	406
4	5,942	2,888	15	93	209
5	2,435	2,276	16	74	166
6	1,919	1,642	17	11	130
7	3,315	1,294	18	8	103
8	2,043	1,019	19	7	81
9	609	1,059	20	6	64
10	479	834	21	4	50
11	528	657			

Specific Mortality Functions

After obtaining a general knowledge of population age structure and average mortality rates, it became possible to examine specific mortality relationships. Drought can result in increased desiccation, predation, and cannibalism mortality in alligators (Hines *et al.* 1968, Spotila *et al.* 1972, Truslow *et al.* 1967). A severe drought can be characterized by a marsh water level of −61 cm (−2.0 feet) for a period of 2 months, and such a drought can increase normal mortality by an estimated 20 percent. An estimated 60 percent of such a drought loss would probably be suffered by 1-year-old animals, 30 percent by 2-year-olds, and the remaining 10 percent by females and other immature males. The adult males inhabit the large bodies of permanent water and would be relatively unaffected by drought. Using these estimates and a September age structure (Table 8), drought mortality rates were calculated for the specified age classes. These rates indicate the percentages by which normal mortality rates are increased during a 2-month drought. These drought rates were simply divided by 2, and monthly rate increases were obtained.

Desiccation.—Alligators have high rates of evaporative water loss and are threatened by desiccation during times of drought (Spotila *et al.* 1972). We estimated that 50 percent of the total drought mortality results from desiccation, while the remaining 50 percent results from predation and cannibalism. The total monthly drought rates were thus divided by 2 to obtain desiccation mortality rates for a month of −61 cm (−2.0 feet) marsh water level. Because of the probable relationship of alligator size to mobility and desiccation vulnerability, the estimated minimum water levels at which no desiccation mortality occurs differ among the three affected age classes. The hypothesized desiccation mortality-water depth relationships have been plotted in Figures 6, 7, and 8.

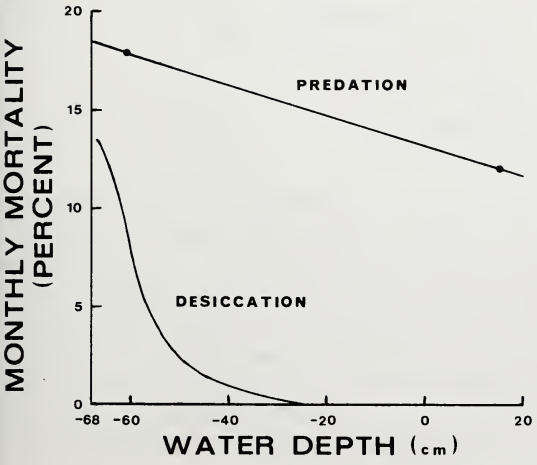

Figure 6.—Relationship between both predation and desiccation mortality and marsh water depth in 1-year-old alligators.

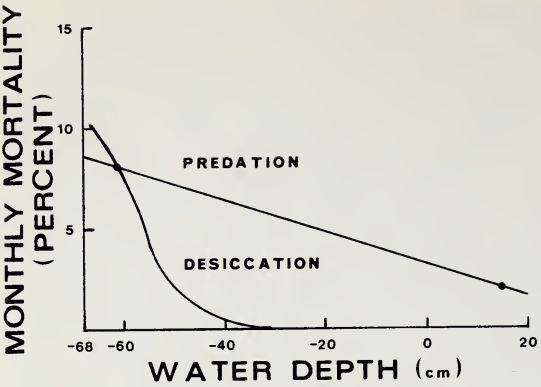

Figure 7.—Relationship between both predation and desiccation mortality and marsh water depth in 2-year-old alligators.

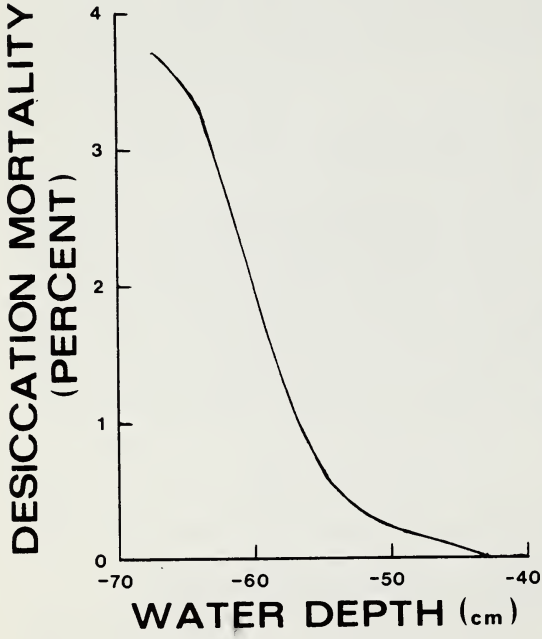

Figure 8.—Relationship between desiccation mortality and marsh water depth in female alligators aged 3-21 years and male alligators aged 3-6 years.

Cannibalism.—Instances of alligator cannibalism have been reported by Kellogg (1929), Giles and Childs (1949), Valentine *et al.* (1972), and Truslow *et al.* (1967), and this mortality source is probably the major density dependent factor operating on Louisiana alligator populations. During years of normal water level cannibalism results in an estimated 2 percent annual mortality rate at present population densities, and in a 6 percent annual mortality rate at carrying capacity densities.

Carrying capacity estimates for the coastal marshland of Cameron and Vermilion parishes are one alligator per five acres of fresh marsh,

one alligator per eight acres of intermediate marsh, and one alligator per 20 acres of brackish marsh. These carrying capacity figures represent population densities on wildlife refuges in the study area with long histories of rigidly protected alligator populations. The total acreage of each marsh type in the study area was divided by the appropriate carrying capacity (acres per alligator) figure. Then, the carrying capacity populations for each marsh type were summed, and a total carrying capacity figure of 147,590 alligators was obtained for the 1,144,600-acre study area.

Assuming that 60 percent of all cannibalism mortality is suffered by 1-year-olds, 30 percent by 2-year-olds, and 10 percent by 3-year-olds, monthly cannibalism mortality rates were calculated for present population densities and carrying capacity densities at average water depths. Present population density was assumed to be about 71,900 (Palmisano *et al.* 1973), and carrying capacity density was again assumed to be 147,590 animals. The density-cannibalism relationship was then plotted (Figure 9). It was assumed that cannibalism would never decrease to 0, and a minimum cannibalism rate was thus arbitrarily set at .001.

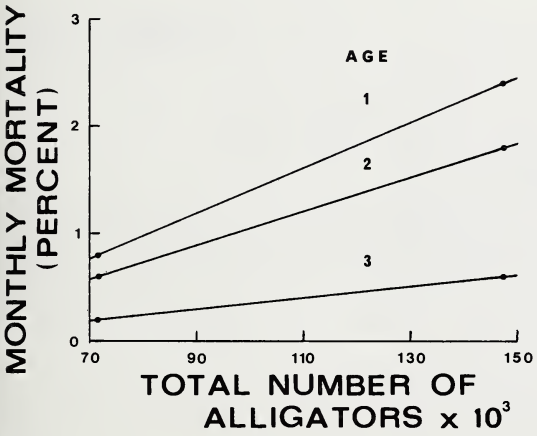

Figure 9.—Relationship between cannibalism mortality and total density in the alligator population of Cameron and Vermilion parishes, Louisiana.

Alligators become concentrated as water levels decline and, during years of severe drought, we estimated 5 and 15 percent cannibalism mortality rates for present density and carrying capacity density populations, respectively. These severe drought cannibalism mortality rates are each 2.5 times as large as average water depth rates for the respective population densities. A severe drought cannibalism rate increase was calculated using annual average water and severe drought cannibalism rate estimates and a September age structure. This total severe drought cannibalism rate increase was then divided by 2 (the number of months involved in a severe drought), and an overall monthly rate increase was obtained.

Age-specific monthly severe drought cannibalism rate increases were

calculated for the three affected age classes using a September age structure and the previously calculated cannibalism rates for average water depth and present density. These age-specific rate calculations invoked the assumption that severe drought cannibalism increases are proportional for the three affected age classes. In this manner, it was calculated that normal monthly cannibalism rates are increased by a factor of 4.65 during months of severe drought. A cannibalism rate multiplier was then plotted by setting 4.65 to correspond with a water level of −61 cm (−2.0 feet), and setting the value 1 to correspond with the average water depth of 15 cm (.5 foot) (Figure 10). A minimum value for this multiplier was arbitrarily assumed to be .25, because it was felt that the cannibalism rate would never decrease to 0.

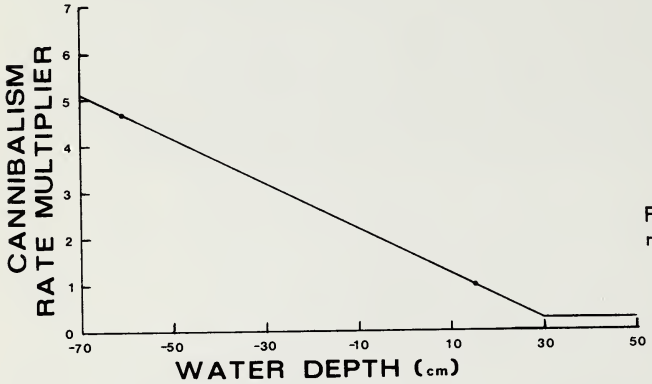

Figure 10.—Cannibalism rate multiplier function.

In the model, the monthly cannibalism mortality rate was determined as a function of density. This rate was then multiplied by the cannibalism rate multiplier, which was determined as a function of monthly water level. The resulting product constituted the increase in mortality due to cannibalism.

Predation.—Alligator young are preyed upon by a wide variety of predators (Neill 1971), and because of the variety it was impossible to incorporate predator densities into the model. Predation rates are probably also a function of alligator density, but again this relationship was not included in the model because of insufficient data. We estimated that during years of average water depths, 1-year-old alligators would suffer approximately a 60 percent loss to predators. We estimated that 2-year-old animals would lose 15 percent annually due to predation. These annual age-specific predation rates were converted to monthly rates in the manner previously described.

During times of drought, alligator young and predators are concentrated in remaining water bodies, and alligators suffer high predation rates (Hines *et al.* 1968). As has been previously mentioned, we estimated that 50 percent of the total alligator mortality suffered during a severe drought (water level at −61 cm for 2 months) could be attributed

to predation and cannibalism. The drought cannibalism rates were determined for each affected age class as previously described, and the drought predation rates were obtained by subtracting the cannibalism rates from the total predation plus cannibalism rates. The predation rate-water depth relationships have been plotted in Figures 6 and 7. It was assumed that predation would never decrease to 0, and minimum monthly predation mortality rates of .05 and .01 were thus set for 1- and 2-year-old alligators, respectively.

Natural Mortality.—In the model, natural mortality is simply an age and sex-specific constant which includes all mortality sources in addition to those already separated from the average mortality values. Natural mortality includes such mortality sources as animals being shot as pests, animals being poached for skin or meat, animals being hit by boats and automobiles and killed accidentally, and animals dying from physiological mortality sources unrelated to drought. Natural mortality rates were obtained by subtracting age and sex-specific cannibalism and predation mortality rates (for months of average water depth) from average total mortality rates. These age and sex-specific rates were then incorporated into the model as constants.

Freeze Mortality.—Chabreck (1965) reported finding dead alligators ranging from .6 to 3.0 meters (2 to 10 feet) in length which had suffocated under ice during a severe freeze in January 1962. Climatological records indicate that in January 1962 the maximum temperature for Lake Charles, Louisiana, was below O°C. for a period of between 2 and 3 days. It was assumed in the model that any drop in maximum temperature below O°C. for a period of 2 days or more would cause alligator freeze mortality. Such a freeze was set to produce a 5 percent loss from the total population and was considered to be neither age nor sex-specific.

Hunting Mortality.—One of the major objectives of this study was to investigate the effects of hunting mortality on alligator populations, and the model included an optional harvest rate which could be applied to the population in September of each year. In the model, the overall optional harvest rate was used to calculate relative age and sex-specific harvest rates similar to those observed in the 1972 and 1973 Louisiana seasons. The calculations involved the use of size and sex-specific harvest percentages which were obtained by summing all wild animals taken in the two Louisiana seasons (from Joanen *et al.* 1972, Palmisano *et al.* 1973, Joanen *et al.* 1973, McNease pers. comm.) and determining the percent composition of this total for each size and sex class (Table 9). The actual calculation of harvest rates in the model is described elsewhere.

Harvest regulations for the 1972 and 1973 seasons were designed to protect mature female alligators. A lower size limit of 1.2 meters (4 feet) total body length was also established to protect young animals. Complete discussions of the regulations governing these two seasons are

Table 9.—Percent composition of the combined 1972 and 1973 Louisiana alligator harvest[a]

Total body length	Males	Females
Meters (feet)	—Percent—	
1.2-1.5 (4-5)	5.93	3.77
1.5-1.8 (5-6)	13.68	6.87
1.8-2.1 (6-7)	14.34	10.30
2.1-2.4 (7-8)	12.99	7.03
2.4-2.7 (8-9)	9.14	1.93
2.7-3.0 (9-10)	6.36	
3.0-3.4 (10-11)	4.64	
3.4-3.7 (11-12)	2.49	
3.7+ (12+)	.53	

[a]Data used to calculate these percentages were taken from Tables 3 and 5 of Palmisano *et al.* (1973), Table 1 of Joanen *et al.* (1973), and a table provided by McNease (pers. comm.). Data on total size composition of harvests were corrected to eliminate farm alligators from the computations.

found in Joanen and McNease (1972d) and Palmisano *et al.* (1973). Since the Louisiana hunters apparently selected for large animals (Palmisano *et al.* 1973), the observed harvest rates will subsequently be referred to as "differential" rates (i.e., differential with respect to size and age).

In the model, it was assumed that alligator populations do not adjust to hunting mortality with compensatory reductions in natural mortality. This assumption was made because of a lack of contrary evidence but may very well be false. Because of the nature of this assumption, our simulated hunting produced maximum detrimental effects on the population.

THE SIMULATION MODEL

Description

A mechanistic mathematical model was constructed to simulate the behavior of the population over time, employing techniques derived from systems science theory as applied to the modeling of ecological systems. The system was defined as the alligator population existing in the area studied, and was divided into components which grouped the population into developmental stages according to age. This was done for each sex. In order to implement the model it was necessary to group the animals in the matrix fashion presented in Table 10, where each element corresponds to a population component. The structure of the model incorporated the use of state equations for each component describing its behavior in terms of stimulus and response variables, the state variable being the number of animals in a particular age and sex class. Initial values for the state variables were chosen for experimental simulations from a set of initial age structures. Behavioral features were

chosen to be the number of deaths (mortality), the number of females which nest (reproduction), and the number of animals leaving the developmental stage (growth). These features were response variables for the population component. The only endogenous stimulus feature used was the number of animals entering the developmental stage through growth or birth. Stimulus variables exogenous to the system were average monthly water levels, temperature, and a harvest rate equal to the percentage of animals taken by hunters.

Table 10.—Grouping of population components

Age of animal[a]	Assigned age class	Subscript for AGEINIT	
		Males	Females
0-1	1	(1,1)	(1,2)
1-2	2	(2,1)	(2,2)
2-3	3	(3,1)	(3,2)
3-4	4	(4,1)	(4,2)
4-5	5	(5,1)	(5,2)
5-6	6	(6,1)	(6,2)
6-7	7	(7,1)	(7,2)
7-8	8	(8,1)	(8,2)
8-9	9	(9,1)	(9,2)
9-10	10	(10,1)	(10,2)
10-11	11	(11,1)	(11,2)
11-12	12	(12,1)	(12,2)
12-13	13	(13,1)	(13,2)
13-14	14	(14,1)	(14,2)
14-15	15	(15,1)	(15,2)
15-16	16	(16,1)	(16,2)
16-17	17	(17,1)	(17,2)
17-18	18	(18,1)	(18,2)
18-19	19	(19,1)	(19,2)
19-20	20	(20,1)	(20,2)
20-21	21	(21,1)	(21,2)

[a]Expressed in years.

The model was basically deterministic and was modified in some experimental simulations to produce a model which was stochastic with respect to environmental factors. Stochastic parameters were monthly water levels and temperature. Values for water levels (expressed in feet) were randomly generated from a normal distribution about the mean for each month (from Table 1). Twelve random numbers between 0 and 1 were generated by a computer library function. The value 6 was subtracted from the sum of these numbers to give a mean value of 0. This number was then multiplied by the standard deviation of the monthly water level (Table 1), and the resulting value was added to the mean value for that month, giving the water level used in the response equations. Temperature was considered only through the use of a factor

representing a freeze during winter, with probability of occurrence equal to .1 (once every 10 years). The freeze factor was designated to occur if the value of one random number generated by the computer library function was less than or equal to .1, where again the range of values was from 0 to 1.

To observe the dynamics of the population over a time period of several years, the month of September was treated as the beginning of a new year, representing T = 1 in the equations below. September was chosen due to the assumption that all eggs were hatched at the end of August. The months November through March were treated as one time block and designated as winter. All rates affecting the stimulus variables were applied during the months April through October unless otherwise designated.

State equations used to describe component behavior were:

(1) [AGEINIT(i,j)](T+DT)= [[AGEINIT(i,j)] (T) x SURNATM X HUNSURV] x DT; for i = 1,21; j = 1,2; and T = 0,11

(2) [AGEINIT(i,j)](T+DT) = [[AGEINIT (i—1,j)] (T)] x DT; for i = 2,21; j = 1,2; and T = 11

(3) [AGEINIT(i,j)](T+DT) = [HACHTOT x .601] x DT; for i =1; j = 1; and T =11

(4) [AGEINIT(i,j)](T+DT) = [HACHTOT x .399] x DT; for i = 1; j = 2; and T = 11

where AGEINIT was the state variable which was used to represent the number of animals in component (i,j), and DT was the time interval, chosen to equal one month. Thus the end of the current month occurred at time T + DT, and DT assumed a constant value of 1.

Monthly Population Changes During April Through October

State variables were updated monthly by state equation (1). SURNATM was a total survival rate including survival from all mortality factors with the exception of harvesting. This rate was determined by the following equation, where APRED was a predation rate for the young, CANNAB was a cannibalism mortality rate, DESS was a desiccation mortality rate, and NATURAL was a natural mortality rate:

SURNATM = 1— (APRED+CANNAB+DESS+NATURAL)

APRED and DESS were computed as functions of average monthly water levels. CANNAB was used as the only density dependent factor in the model, and thus a function of the total population (CANN) was computed and then multiplied by a factor (CANNMUL) which was determined as a function of the average monthly water level. The above rates were determined by the following equations, where WATER corresponded to the average monthly water level (expressed in feet),

and TOTAL was equal to the total population. All rates not applicable to a component were assigned default values which were set so as to have no influence on the function value.

CANNMUL = −1.46(WATER) +1.73 (see Figure 10)
CANNAB = CANNMUL (CANN)

Response equations for age class 1:

APRED = −.0236 (WATER) +.1318 (see Figure 6)
for WATER≤3.46

APRED = .05 (see Figure 6)
for WATER>3.46

CANN = .00000021 (TOTAL) −.0071 (see Figure 9)
for TOTAL>38600

CANN = .001 (see Figure 9)
for TOTAL≤38600

Response equations for age class 2:

APRED = −.0240 (WATER)+.0320 (see Figure 7)
for WATER≤.91

APRED = .01 (see Figure 7)
for WATER>.91

CANN = .00000016 (TOTAL) −.0055 (see Figure 9)
for TOTAL>40600

CANN = .001 (see Figure 9)
for TOTAL≤40600

Response equations for age class 3:

CANN = .00000005 (TOTAL)−.0016 (see Figure 9)
for TOTAL>52000

CANN = .001 (see Figure 9)
for TOTAL≤52000

In addition to the above rates, NATURAL was applied to all age classes, and DESS was applied to males in age classes (1-6) and to all females. Natural mortality rates (NATURAL) are presented in Table 11 and were calculated as previously described. DESS values were derived from Figures 6, 7, and 8 and were included in the model in tabular form.

HUNSURV was a survival rate obtained from harvest mortality rates and was applied to age classes (4-21) during the month of September only. Calculation of these survival rates involved a series of steps in the model. First, a total was obtained for all animals of harvestable size (ages 4-21). The total number of harvestable animals was then multiplied by the desired overall hunting rate (HUNRATE) to obtain the total number of animals to be harvested from all age classes (HARTOT). The next step involved the use of size and sex-specific harvest percentages (see Table 9) which were read into the program as HUNTING (I). In the model, HUNTING (I) was multiplied by HARTOT to obtain the number of animals to be harvested from each size and sex class (HARNUM (I)). The values for HARNUM(I) were then subtracted from the

Table 11.—Natural mortality rates

Age class	NATURAL Males	NATURAL Females	Age class	NATURAL Males	NATURAL Females
1	.011	.011	12	.043	.020
2	.044	.044	13	.043	.020
3	.031	.031	14	.043	.020
4	.033	.033	15	.043	.020
5	.033	.033	16	.043	.020
6	.033	.033	17	.043	.020
7	.033	.033	18	.043	.020
8	.033	.033	19	.043	.020
9	.043	.020	20	.043	.020
10	.043	.020	21	.043	.020
11	.043	.020			

number of animals comprising each size and sex class (TOTSIZE(I)) to obtain the number of hunting survivors. The number of survivors was divided by TOTSIZE (I) to obtain hunting survival rates for each size and sex class (SURHUNM (I,J)). HUNSURV was finally set equal to the SURHUNM values of the appropriate age and sex classes.

Monthly Changes During November Through March

At the beginning of winter, T (see state equation 1) was automatically incremented by 4DT to give the value T = 7, which represented the end of March, and the state variables were updated. It was assumed that the only rate affecting the population component during this time period was a freeze mortality. If the freeze factor was applied, SURNATM was set to equal 95 percent for each component. If no freeze occurred, there was no change in the population.

Yearly Population Changes

State equation (2) was used to update the state variables for age classes (2-21) at the end of each year. The number of animals leaving a component became the number of animals entering the next developmental stage. The last age class was simply "dropped" due to the assumption that no animals survived past age 21.

State equations (3) and (4) were used to compute the number of male and female hatchlings, respectively. HACHTOT represented the total number of eggs hatched, and was expressed by the following equation:

$$\text{HACHTOT} = [(\text{EGGS}(1-\text{NESTFLD})) \times (1-\text{PRED})] \times .768$$

Rates contained in this equation were applied at the end of August.

EGGS was used to represent the total number of eggs laid, NESTFLD was a rate which represented egg mortality due to nest flooding, and PRED was a raccoon nest predation rate. A survivorship constant equal to 76.8 percent was applied to all eggs surviving predation and nest flooding. EGGS was computed by summing the number of eggs produced by each adult female age class (classes (9-21)), which was dependent upon the population component size (AGEINIT) and nesting effort (NESTEFF). NESTEFF was used to represent the percentage of females which nest (reproductive rate) as a function of the average water depth for May and June. This rate was applied only at the end of June, when it was multiplied by the number of females in each reproducing class to yield the total number of nesting females in that class (REPRATE). REPRATE was then multiplied by the average number of eggs laid per female, which was assumed to be 38.9, giving total eggs produced by that population component. The percentage of eggs lost due to flooding of nests (NESTFLD) was determined to be a function of the maximum value of June, July, and August water depths. NESTFLD attained values derived from Figure 4. Equations used to describe raccoon predation on the eggs as a function of August water levels were:

PRED = .035 (see Figure 5)
for WATER<.2 or WATER>1.2

PRED = .55 (WATER)−.075 (see Figure 5)
for .2≤WATER≤.8

PRED = −.825 (WATER)+1.025 (see Figure 5)
for .8<WATER≤1.2

The number of male hatchlings was assumed to be 60.1 percent of the total, and the number of females was assumed to be 39.9 percent. These rates were multiplied by HACHTOT to give the number of males and females entering the first age class.

The new age structure resulting at the end of the simulated year became the new initial age structure for the start of the next year.

Implementation

The model was implemented by a Fortran program on the Control Data 6500 computer system. Block diagrams for the computations are shown in Figure 11. A complete listing of one version of the program is contained in the Appendix, Pages 55-59.

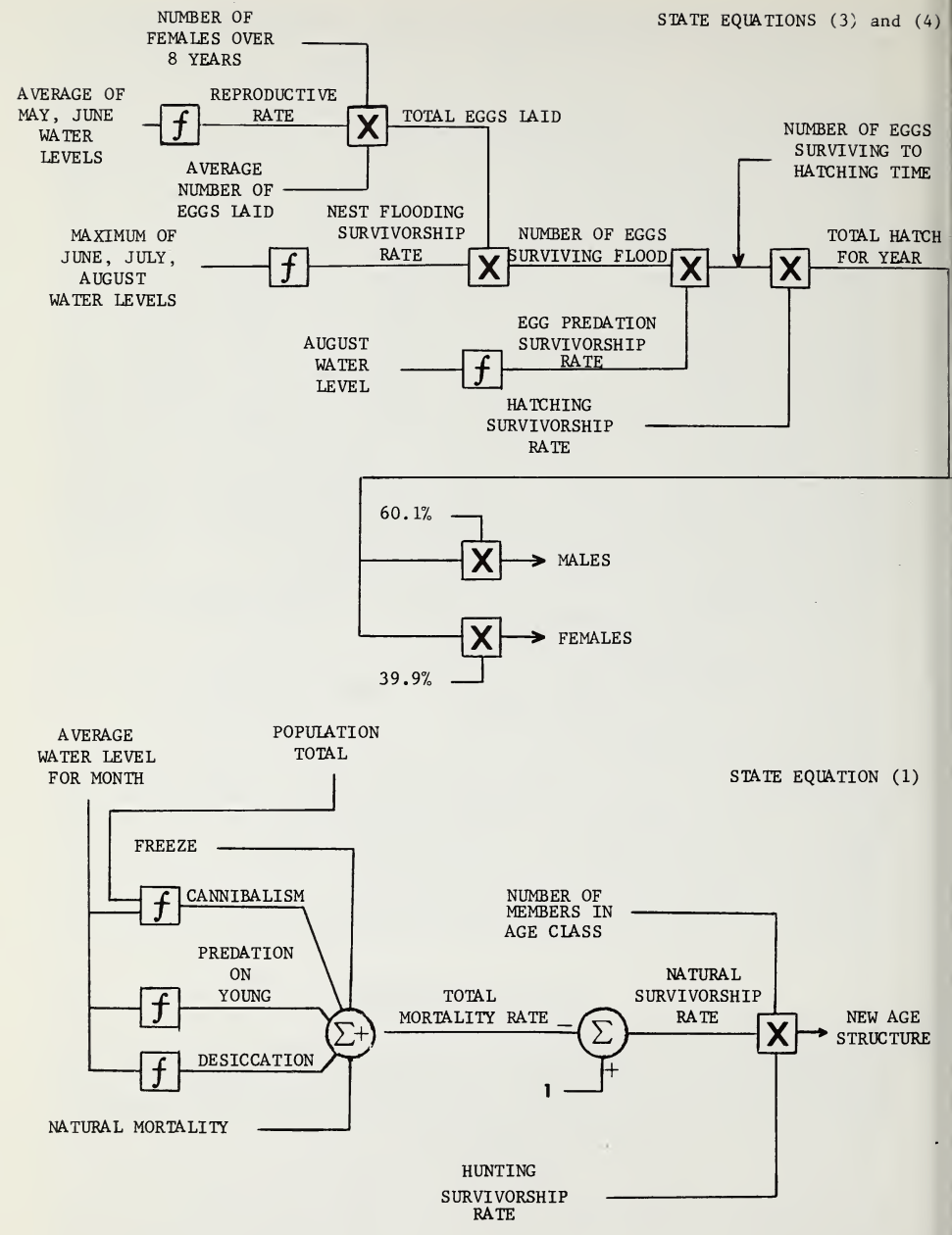

Figure 11.—Block diagram of model state equations.

RESULTS AND DISCUSSION

Alligator Population Structure

Preliminary population growth simulations were run using a September initial age structure (Table 8) calculated from Chabreck's (1966) observed May-June size structure. Results of one such 20-year simulation with constant 15 cm (.5 foot) water depths are presented in Figure 12. Irregularities in this population growth curve (Figure 12) resulted from inadequacies or inconsistencies in the initial age structure. The high population growth rate for year 1 can be directly attributed to the introduction of a "normal" complement of hatchlings at the end of that year. The other major irregularity in the population growth curve occurred during year 9, the year in which hatchling females from the initial age structure reached sexual maturity. Simulation results thus suggested an inadequate representation of animals in the first age class of the initial age structure. Analysis of Chabreck's (1966) field data provided additional support for the contention that hatchlings were underestimated in the derived September age structure. Calculations assuming (1) average egg mortality and hatching success (from Joanen 1969), (2) equivalent hatchling mortality rates from September to May and from June to September, and (3) a stable age distribution (this had probably not been achieved), yielded an unrealistically low number of 1-year-old survivors for September 1966.

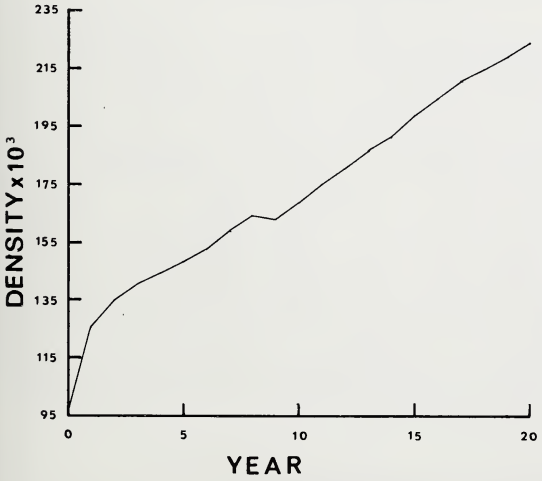

Figure 12.—Simulated population growth using the September initial age structure shown in Table 8. Water depths were held constant at 15 cm (.5 foot) and no winter freezes occurred.

Because of this apparent underrepresentation of hatchlings, the use of the Table 8 age structure in experimental simulations would have caused problems in interpreting population response curves. For example, it would have been difficult to separate effects of the irregular age structure from effects of experimental manipulations (such as variations

in hunting pressure or environmental parameters) in such response curves. Therefore, the initial proportions of animals in each age and sex class for all subsequent computer runs were based on the population structure generated by the 20-year simulation (Figure 12). An example of this computer-generated age structure is shown for an initial population of 100,000 in Table 12.

Table 12.—Computer-generated initial age structure for a population of 100,000

Age	Males	Females	Age	Males	Females
1	30,551	20,283	12	353	386
2	8,962	5,950	13	273	353
3	4,733	3,142	14	201	306
4	3,587	2,382	15	138	248
5	2,777	1,844	16	100	214
6	2,140	1,421	17	73	183
7	1,660	1,102	18	53	158
8	1,289	856	19	39	136
9	996	661	20	29	118
10	710	557	21	12	53
11	504	467	Total	59,180	40,820

Model—Field Data Comparison

Nest counts conducted in the years 1970-1973 (Joanen and McNease 1970b, 1972c, 1973b; Palmisano *et al.* 1973) provided an opportunity to test the model against observed field data. A computer-generated initial age structure was constructed such that the number of nests produced the first year (using observed 1969-1970 marsh water depths) closely approximated the 1970 aerial nest count (percent error = .08). The simulation was then run for three additional years with observed 1970-1973 water depth inputs (Table 1), and the number of nests generated was compared with field observations for 1971, 1972, and 1973 (Figure 13). The errors between simulated and observed data for these 3 years were 3.13, 9.92, and 22.70 percent, respectively. Considering possible initial differences in age structure and the unusually large fluctuation in nests over these years, the response of the model seemed reasonably good.

Water Level Fluctuations

In order to test the behavior of the model, several deterministic simulations were run using varied water levels. One such series of 2-year runs is shown in Figure 14. In each of these runs, the water depth in a selected month during the first year was set at either 0 or 30 cm

(1 foot), with water depths for other first year months and all second year months held constant at 15 cm (.5 foot). The difference between the two September runs can be attributed to higher predation, canni-

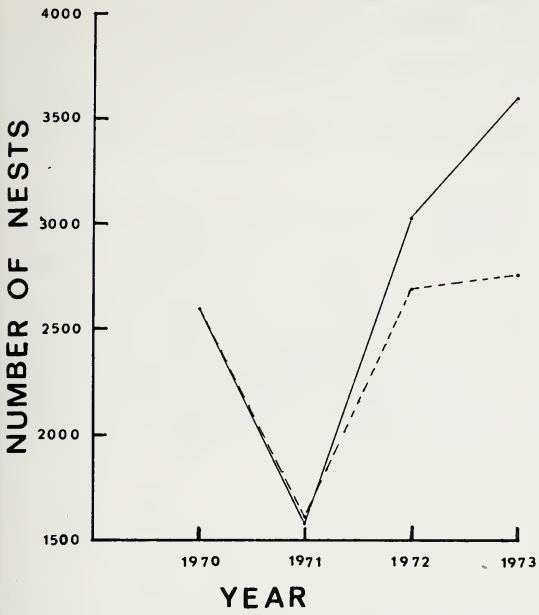

Figure 13.—Comparison of simulated nests (dashed line) with observed nest count data, 1970-1973 (solid line).

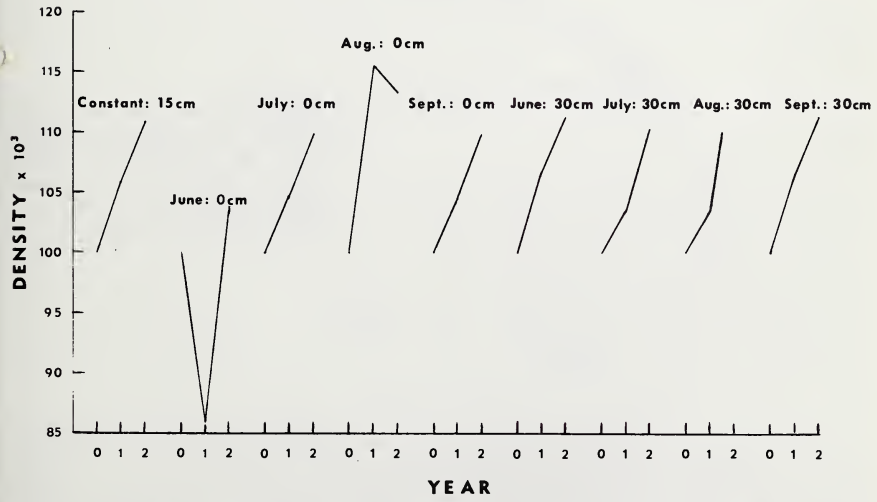

Figure 14.—Series of 2-year simulations demonstrating population response to varied marsh water depths in single selected months. The varied water depths occurred in selected months during the first year, and depths for all other months were held constant at 15 cm (.5 foot).

balism, and desiccation rates in the low water run. Zero water level in June resulted in a substantial population decrease as a consequence of poor nesting effort, although a recovery was made in the following year. Thirty cm (1 foot) water depths in July and August resulted in population declines attributable to nest flooding. Zero water level in August caused a large population increase as a consequence of lowered nest predation and a resultant high number of September hatchlings. Normal predation and increased cannibalism the following year reduced the population, however, primarily by removing large numbers of first year animals.

Population response to hurricane (100 percent nest flooding) and severe drought (increased cannibalism, predation, and desiccation) are shown in Figure 15. The hurricane was simulated with 122 cm (4 feet) water depths in August, and the severe drought was represented by −61 cm (−2 feet) water levels in both June and July. In these 5-year deterministic simulations, the severe weather conditions occurred in year 1, and all water depths were set at 15 cm (.5 foot) for the remainder of each run. The rapid population recoveries from both drought and hurricane were of particular interest.

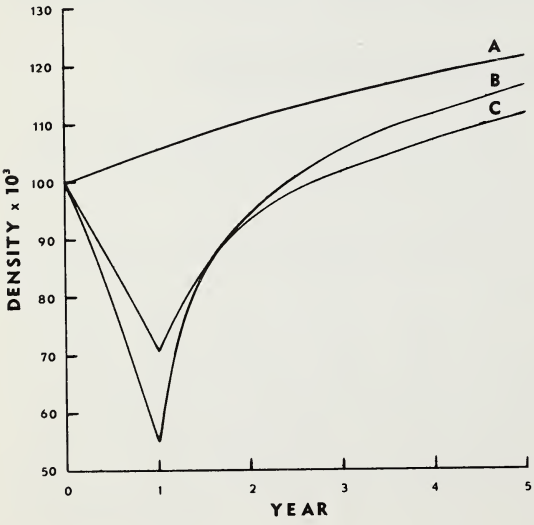

Figure 15.—Simulated population response to August hurricane (plot B) and severe summer drought (plot C). A constant water depth simulation (plot A) is provided for comparison.

The effects of weather were further investigated through the use of environmentally stochastic simulations. In these stochastic runs, monthly water depths were randomly generated from a normal distribution about the mean level for each month (from Table 1). The stochastic modifications also included the .1 probability of a winter freeze each year. Results of two stochastic runs and one deterministic [monthly water lev-

els set at 15 cm (.5 foot), no winter freezes] simulation are shown in Figure 16. It is interesting to note that alligator numbers in the environmentally stochastic simulations exceeded the constant water level population during some years. Age structures generated by the 20-year stochastic runs were extremely irregular and thus seem to preclude the reasonable use of time-specific life table methods in the study of wild alligator populations.

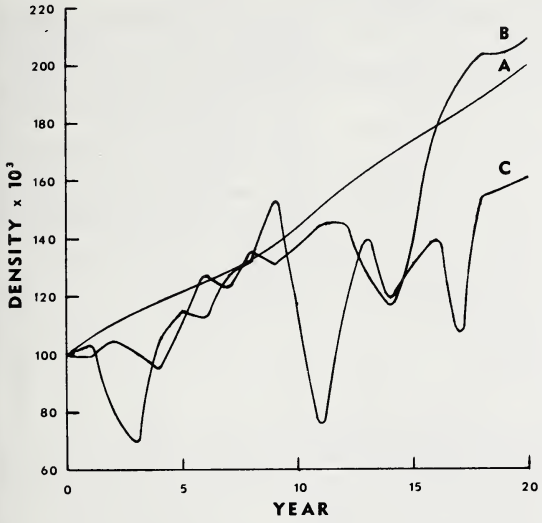

Figure 16.—Simulated population response to constant (plot A) and randomly generated (plots B and C) marsh water depths and winter freezes.

Alligator Harvest Strategies

Differential Harvest Rates

One of the major objectives of this study was to examine the effects of various harvest strategies on alligator populations. This investigation was begun with a series of deterministic simulations [constant water at 15 cm (.5 foot), no freezes] designed to demonstrate population response to various differential hunting rates (Figure 17). Again, these rates applied to animals of harvestable size (aged 4-21 years), rather than to the entire population. Calculations based on these simulations indicated that a harvest rate of approximately 5.28 percent will maintain a base population of 100,000 alligators for at least 20 years. It must be emphasized that the effects of these specific harvest rates on the simulated population should not be generalized to wild alligators. It has been shown that the simulated population does not increase as rapidly as the actual population being modeled (Figure 13), and the real population would thus be expected to tolerate slightly greater harvest rates than the simu-

lated one. The relationships between various harvest rates under different harvest strategies, however, are particularly important.

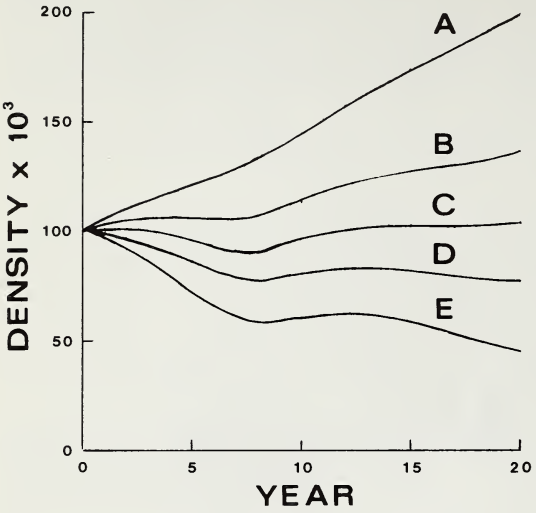

Figure 17.—Simulated population response to various differential harvest rates: plot A = no hunting, plot B = 3 percent, plot C = 5 percent, plot D = 7 percent, plot E = 10 percent. In each simulation water depths were held constant at 15 cm (.5 foot) and no winter freezes occurred.

Another series of deterministic simulations [constant water at 15 cm (.5 foot), no freezes] was run to examine the response of various initial populations to an annual 5 percent hunting rate. The simulations were compared by plotting percent deviation from initial population size versus time (Figure 18). The smaller base populations grew at faster rates than larger populations because of the density dependent effects of

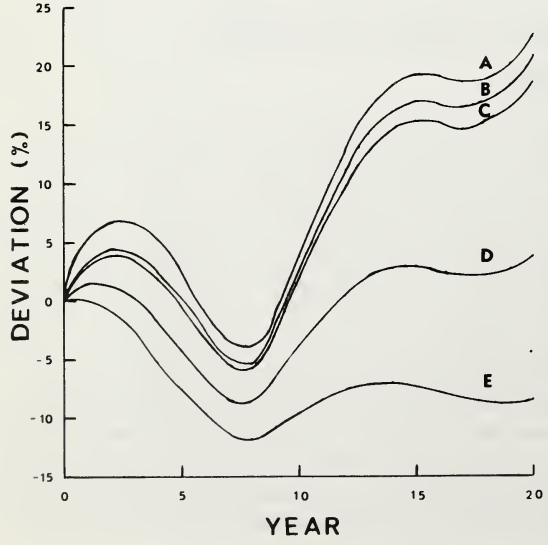

Figure 18.—Simulated response of various initial populations to an annual 5 percent differential harvest rate. Percent deviation from initial population size is plotted for the following initial densities: plot A = 1,000, plot B = 10,000, plot C = 50,000, plot D = 100,000, plot E = 150,000. In each simulation water depths were held constant at 15 cm (.5 foot) and no winter freezes occurred.

cannibalism. It was calculated than an initial population of approximately 115,450 should be maintained for at least 20 years under an annual 5 percent differential hunting regime.

Two stochastic simulations were run to examine the effects of randomly varying water levels and winter temperatures as found in Louisiana on hunted alligator populations. Comparison of these stochastic simulations with a constant water level [15 cm (.5 foot)] simulation (Figure 19) suggested that management strategies should not be based upon assumed average water depths (and thus upon assumed average recruitment and survival rates), but that important environmental parameters should be monitored and considered in the formulation of management plans.

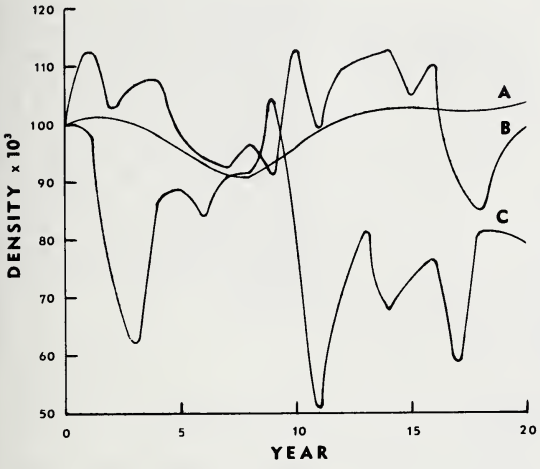

Figure 19.—Simulated population response to an annnual 5 percent differential harvest rate with constant (plot A) and randomly generated (plots B and C) marsh water depths and winter freezes.

A 20-year deterministic simulation with 5 percent differential hunting (Figure 19, plot A) yielded a population which was 48.11 percent smaller than a 20-year non-hunted population (Figure 16, plot A). Simulations of a hunted population (Figure 19, plot C) and a non-hunted population (Figure 16, plot C) were also run using an identical set of randomly generated water levels and winter freezes. In this case, the hunted population was 49.92 percent smaller than the non-hunted population, indicating that hunting may be slightly more detrimental to populations subjected to fluctuating water levels.

Periodic Harvest

Computer simulations of big game populations in which individual female productivity increases with age, suggest that harvests every 2-4 years can increase yields by 10-20 percent (Walters and Bandy 1972). Deterministic simulations were run to evaluate this harvest strategy with respect to alligator populations. These simulations included: (1) harvest-

ing alligators at a 5 percent differential rate every year, (2) harvesting animals at a 10 percent differential rate every second year, and (3) harvesting animals at a 15 percent differential rate every third year (see Figure 20). Valid comparisons of population size under these harvest regimes can be made in years 6, 12, and 18. The periodic harvests did not maintain base populations at the level produced by annual hunting, and did not result in increased yields of alligator hide. Periodic harvesting was thus concluded to be ineffective as a management strategy, possibly because female alligator productivity does not increase with age.

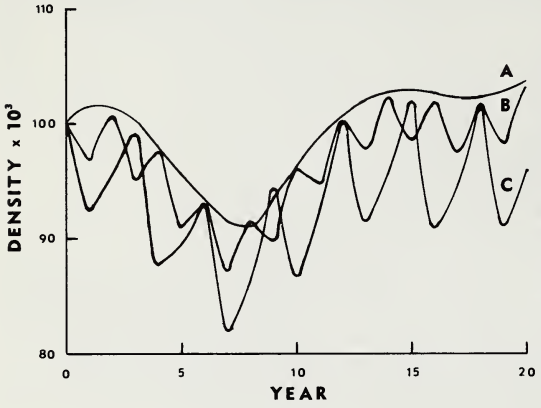

Figure 20.—Simulated population response to periodic harvesting under differential rates. Simulations included harvesting at a 5 percent rate every year (plot A), harvesting at a 10 percent rate every second year (plot B), and harvesting at a 15 percent rate every third year (plot C). In each simulation water depths were held constant at 15 cm (.5 foot) and no winter freezes occurred.

Proportional Harvest Rates

In an attempt to investigate possible means of increasing annual yield, deterministic simulations were run using equal harvest rates for all size classes within a given sex (the 75:25 observed male to female harvest ratio was retained). Such harvest rates are dependent on hunters taking animals in proportion to their relative abundance in the population and will thus be termed "proportional."

The results of 5, 9, 10, and 15 percent proportional hunting rates are presented in Figure 21 and can be compared with differential rates shown in Figure 17. Results of simulations with 5 percent differential and proportional harvest rates are plotted in Figure 22 for direct comparison of effects on population growth. Linear meters and feet of hide taken in selected years at various differential and proportional harvest rates were also calculated (Table 13). The ratio of square feet to linear feet of hide increases with increasing total body length in alligators. Alligator buyers are interested in square feet of hide and thus compensate for this difference by paying higher prices per foot for hide of larger animals. The annual incomes derived from the simulated harvests were thus calculated using two different price schedules, and these values are shown for selected years in Table 14.

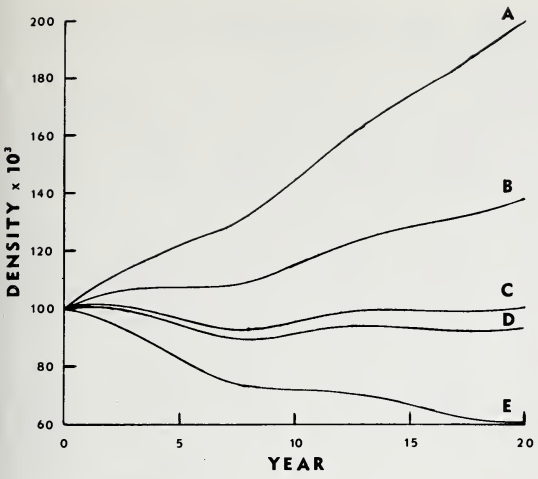

Figure 21.—Simulated population response to various proportional harvest rates: plot A = no hunting, plot B = 5 percent, plot C = 9 percent, plot D = 10 percent, plot E = 15 percent. In each simulation water depths were held constant at 15 cm (.5 foot) and no winter freezes occurred.

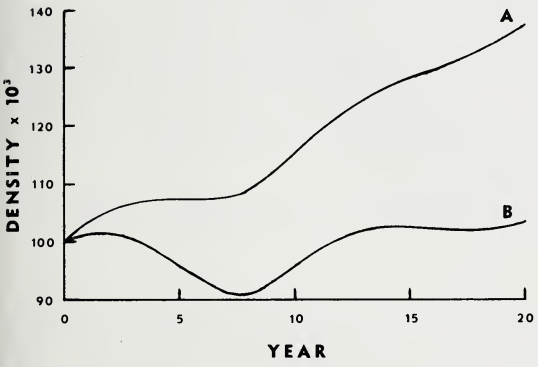

Figure 22.—Simulated population response to annual 5 percent proportional (plot A) and 5 percent differential (plot B) harvest rates. In each simulation water depths were held constant at 15 cm (.5 foot) and no winter freezes occurred.

Table 13.—Yield in hide for selected years under various harvest regimes[a]

Harvest regime	Year 1		10		20	
	——————Linear meters (feet) of hide——————					
3 percent differential[b]	1,580	(5,185)	1,950	(6,399)	2,298	(7,539)
5 percent differential	2,635	(8,646)	2,845	(9,335)	3,062	(10,045)
7 percent differential	3,693	(12,115)	3,213	(10,542)	3,151	(10,338)
10 percent differential	5,269	(17,288)	3,511	(11,520)	2,910	(9,548)
5 percent proportional[c]	2,328	(7,639)	2,640	(8,663)	3,071	(10,075)
9 percent proportional	4,186	(13,735)	3,862	(12,670)	3,950	(12,960)
10 percent proportional	4654	(15,269)	4,081	(13,389)	4,048	(13,280)
15 percent proportional	6,978	(22,893)	4,717	(15,476)	3,904	(12,809)

[a]Initial population in each case is 100,000.

[b]Population response curves for differential harvest regimes are shown in Figure 17.

[c]Population response curves for proportional harvest regimes are shown in Figure 21.

Table 14.—Derived income from alligator hide sales for selected years under various harvest regimes[a]

Harvest regime	Year 1		Year 10		Year 20	
	Price sched.1[b]	Price sched.2[c]	Price sched.1	Price sched.2	Price sched.1	Price sched.2
	—Dollars—					
3 percent differential[d]	76,575	60,834	94,485	75,078	111,335	88,470
5 percent differential	127,686	101,448	137,803	109,518	148,333	117,858
7 percent differential	178,918	142,158	154,548	123,444	151,735	121,104
10 percent differential	255,316	202,866	168,149	134,748	139,329	111,660
5 percent proportional[e]	111,251	85,206	125,055	95,406	145,485	110,712
9 percent proportional	200,002	153,156	182,081	138,270	186,146	140,814
10 percent proportional	222,369	170,304	192,233	145,782	190,581	143,934
15 percent proportional	333,379	255,312	221,154	166,524	182,821	136,878

[a]Initial alligator population in each case was 100,000. Corresponding harvest yields expressed in linear meters and feet of hide are shown in Table 13.

[b]Price schedule 1 corresponds to prices paid for alligators taken during the 1973 harvest season. Prices were $14.00 per foot for 4, 5, and 6 feet alligators, $15.00 per foot for 7 and 8 feet alligators, and $16.00 per foot for animals 9 feet and larger (Mirandona Brothers pers. comm.).

[c]Price schedule 2 corresponds to predicted future hide prices. Predicted prices are $7.50 per foot for 4 feet alligators and $12.00 per foot for animals 5 feet and larger (Mirandona Brothers pers. comm.).

[d]Population response curves for differential harvest regimes are shown in Figure 17.

[e]Population response curves for proportional harvest regimes are shown in Figure 21.

The proportional harvest strategy appeared to be highly successful, and, with respect to population growth, a 9 percent proportional rate was virtually equivalent to a 5 percent differential rate. The 9 percent proportional rate, however, yielded a much greater amount of hide and resulting income than the 5 percent differential rate (Tables 13 and 14). It thus appears that alligator populations can withstand a much higher rate of proportional than differential hunting, and that higher proportional rates can result in increased yield of hide.

Taking different sized animals in proportion to their abundance in the population is a management strategy which should be relatively easy to implement. In 1972, alligators taken by shooting were generally in the smaller size classes (Palmisano *et al.* 1973), probably because of the larger number of small animals in the hunted population. Fishing with a baited line, however, appeared to catch the larger animals, and this resulted in part from the intentional placement of baited hooks high above the water surface (Palmisano *et al.* 1973). Regulations could be imposed to lower the heights of alligator hooks above the water, thus giving animals of various sizes an equal opportunity to strike. Also, shooting or live-trapping, as described by Chabreck (1963), could be employed, thus enabling hunters to select certain size classes.

Egg Collection Management

Collecting and artifically incubating eggs, distributing hatchlings, and rearing young animals has been reported to be a successful management strategy for crocodiles (*Crocodylus niloticus* Laurenti) in South Africa (Pooley 1969, 1971) and Rhodesia (Blake 1970). This type of management program was examined for alligators through the use of deterministic and stochastic simulations. In the simulations, 10,000 eggs were "collected" in early July each year, and the young alligators were released in September after either one or two years of rearing. A 75 percent hatching rate was assumed for the artificially incubated eggs (Chabreck unpubl. data), and first and second year annual mortality rates for reared young were assumed to be 10 and 5 percent, respectively. Pen-reared alligators respond similarly to wild alligators when transferred to new locations and released (Chabreck 1971a). In the model, pen-reared alligators which were reintroduced to the population were thus assumed to be qualitatively similar to wild alligators of the same age.

Collecting eggs and rearing and releasing young alligators appears to be a very effective management strategy as indicated by deterministic simulations (Figure 23). After 20 years, the 1- and 2-year rearing pro-

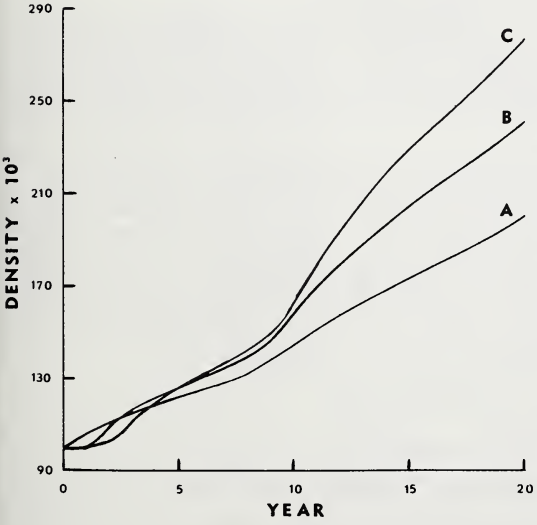

Figure 23.—Simulated population response to egg collection management programs. Plot A corresponds to no management. Plot B corresponds to a management program in which 10,000 eggs were collected annually, and hatchlings were reared for 1 year and released. Plot C corresponds to a management program in which 10,000 eggs were collected annually, and hatchlings were reared for 2 years and released. In each simulation water depths were held constant at 15 cm (.5 foot) and no winter freezes occurred.

grams resulted in populations which were 20.37 and 38.23 percent, respectively, larger than the unmanaged population. The managed populations began to diverge rapidly from the unmanaged population during year 9, the year in which the first group of artificially raised females reached sexual maturity.

An egg collection management program with one year of rearing young was also simulated using the same set of randomly generated water levels and winter freezes used for the unmanaged population shown in Figure 16, plot C. Under this particular set of environmental conditions, the managed population was 26.32 percent larger than the unmanaged population at the end of 20 years. This difference between managed and unmanaged populations was considerably larger than the difference (20.37 percent) indicated by the deterministic simulations. Thus, it appears that the beneficial effects of an egg collection management program are increased during periods of wide water level fluctuations. This conclusion was expected, since egg collection management results in the protection of eggs and first year animals, which suffer the greatest increases in mortality during periods of changing water levels.

Simulation can be used in the economic analysis of possible management options. For example, simulations indicated that the addition of an egg collection management program (one year of rearing young) to a 7 percent differential harvest regime resulted in maintenance of the base population after a period of 20 years, while a similarly hunted but unmanaged population decreased considerably (Figure 24). The num-

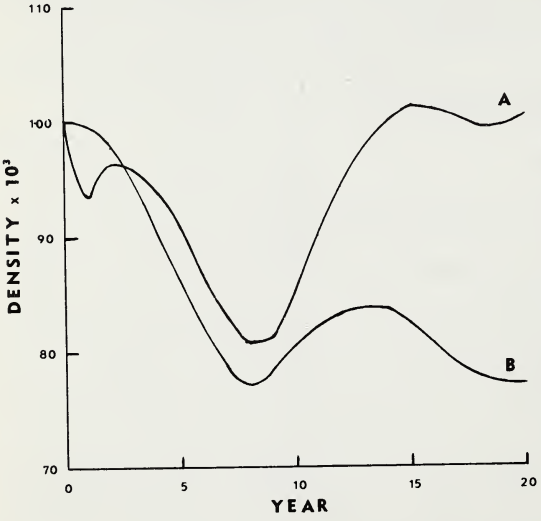

Figure 24.—Simulated population response to an annual 7 percent differential harvest rate with and without egg collection management. Plot A corresponds to a management program in which 10,000 eggs were collected annually, and hatchlings were reared for 1 year and released. Plot B corresponds to no egg collection management. In each simulation water depths were held constant at 15 cm (.5 foot) and no freezes occurred.

bers of linear meters and feet of hide harvested each year under a 7 percent differential harvest regime with and without egg collection management were calculated and are presented in Table 15. The egg collection management program resulted in a total increase in yield of 13,629 meters (44,713 feet) of hide over the unmanaged population. Using an average 1973 price of $13.13 per linear foot (Joanen *et al.* 1973), the increased yield results in a total difference of approximately $587,100. This increased revenue reduces to approximately $29,400 per year.

Table 15.—Yield in hide from 7 percent differentially harvested alligator populations with and without an egg collection management program[abc]

Year	Egg collection management	No management
	——————Linear meters (feet) of hide——————	
1	3,693 (12,115)	3,693 (12,115)
2	3,597 (11,801)	3,590 (11,779)
3	3,629 (11,907)	3,626 (11,897)
4	3,841 (12,602)	3,836 (12,585)
5	4,235 (13,894)	3,918 (12,854)
6	4,453 (14,609)	3,918 (12,854)
7	4,435 (14,549)	3,815 (12,515)
8	4,178 (13,708)	3,564 (11,693)
9	4,045 (13,272)	3,343 (10,968)
10	3,942 (12,934)	3,213 (10,542)
11	3,857 (12,653)	3,144 (10,316)
12	3,874 (12,710)	3,107 (10,193)
13	3,951 (12,962)	3,105 (10,188)
14	4,015 (13,174)	3,170 (10,399)
15	4,157 (13,640)	3,307 (10,851)
16	4,388 (14,396)	3,352 (10,998)
17	4,512 (14,802)	3,354 (11,005)
18	4,571 (14,998)	3,328 (10,919)
19	4,592 (15,067)	3,282 (10,768)
20	4,480 (14,697)	3,151 (10,338)
Total	82,445 (270,490)	68,817 (225,777)

[a]Initial population in each case is 100,000.

[b]Population response curves are shown in Figure 24.

[c]Egg collection management program included collecting and hatching 10,000 eggs annually and rearing young for one year before reintroduction.

The cost of an egg collection management program would probably prohibit such an operation if it was conducted on a strictly economic basis. The cost of rearing 7,500 alligators to age 1 would be about $38,000. The estimated cost of major expenditures would be: food, including vitamin and mineral supplements, $5,000 (Coulson *et al.* 1973); labor, $18,000; equipment and supplies, $10,000; facilities, depreciated over a 20-year period, $5,000. An egg collection program would thus not be economically justifiable in the situation described. However, similar economic analyses can be applied to a wide variety of situations involving different harvest and management options, and the above example was simply provided to demonstrate the utility of simulation for such analyses.

SUMMARY AND CONCLUSIONS

A model was constructed to simulate the dynamics of the alligator population inhabiting the privately owned marshland of Cameron and Vermilion parishes, Louisiana. The model was used to examine the consequences of various management strategies and the effects of variable environmental parameters on the alligator population.

Data used to construct the model were assembled from a variety of published and unpublished sources. In some cases, it was necessary to rely upon estimates based on field observations of wild alligators in the study area. The general approach to the model was to sacrifice statistical rigor, when necessary, in order to obtain a reasonably complete model. As a result, the model is believed to include most of the relationships affecting the studied alligator population, although knowledge of the exact nature of some of the included functions will require further field research.

During the construction of the model, it became evident that numerous important phases of alligator population biology have been either inadequately studied or completely neglected. We, therefore, recommend that additional research effort be expended on the following functional relationships affecting alligators: (1) growth rates of wild alligators and effects of food intake and temperature on these rates; (2) the relationship between the percentage of female alligators nesting and marsh water depth; (3) the relationship between nest flooding rates and marsh water depth; (4) the interrelationship between nest predation, raccoon density, and marsh water depth; (5) the effects of population density and marsh water depth on cannibalism rate; (6) the effects of predator density and marsh water depth on predation rates of young alligators; and (7) the relationship between desiccation mortality and marsh water depth. Obviously, this is not an exhaustive list of possible alligator research topics, but it does include the relationships which appeared to be of primary importance to the studied population.

In the model, nesting effort, nest flooding, desiccation mortality, and predation on alligator eggs and young were all determined as functions of monthly water depth averages. Cannibalism was considered to be the major density dependent factor operating on the population and was determined as a function of total population density and marsh water depth. The model contained a freeze mortality which was based on minimum winter temperatures. In addition, the model included a harvest option which resulted in alligator hunting mortality.

A mechanistic mathematical model was constructed to simulate the behavior of the population over time. The modeled system was defined as the alligator population existing in the study area and was divided into components according to age and sex. In the model, animals were grouped in a matrix fashion, with each element corresponding to a population component. The structure of the model incorporated the use of state equations which described the behavior of each component in

terms of stimulus and response variables. State variables were defined as the number of animals in each age and sex class. The model was basically deterministic but included an optional stochastic modification which produced random monthly water depths and winter temperatures.

The model was tested by means of a simulation with observed 1970-1973 monthly marsh water depths. Alligator nest counts were conducted in the study area during these years, and the numbers of nests produced by the simulated population were compared with these field observations. The errors between simulated and observed data for the years 1971-1973 were 3.13, 9.92, and 22.70 percent, respectively.

The behavior of the model was tested using deterministic simulations with various water depth inputs for selected months. Zero water level in June produced an especially significant result, causing a substantial population decrease attributable to poor nesting effort and a resultant small number of hatchlings. Simulations of an August hurricane and a summer drought each produced substantial population declines, although rapid recoveries occurred in both cases. Environmentally stochastic simulations produced extremely irregular population response curves with high year-to-year variation in density. Age structures generated by the stochastic simulations were also irregular and seemed to preclude the reasonable use of time-specific life table methods on the studied alligator population.

Deterministic simulations using various differential hunting rates indicated that a base population of 100,000 alligators should be maintained for 20 years when subjected to an annual hunting rate slightly greater than 5 percent. Deterministic simulations also indicated that small base populations can withstand greater hunting rates than larger populations because of the density dependent effects of cannibalism. Environmentally stochastic simulations indicated that harvest strategies should not be based on assumed average recruitment and survival rates, but that important environmental parameters should be monitored and considered in the formulation of management plans.

Deterministic simulations indicated that periodic harvesting is an ineffective management strategy for the simulated alligator population. Experimental simulations were run using equal harvest rates for all size classes within a given sex (proportional hunting). Comparisons of population response curves for simulations with equivalent differential and proportional hunting rates indicated that much greater population increases are possible with proportional hunting. Nine percent proportional hunting and 5 percent differential hunting produced similar population response curves, although the 9 percent proportional hunting yielded a greater amount of alligator hide. The proportional harvest strategy thus appeared to be highly successful, and recommendations were made for implementation of such a strategy.

Deterministic simulations with egg collection management programs produced greater population increases than similar simulations with no

management. Stochastic simulations indicated that the beneficial effects of egg collection management are enhanced during periods of wide water level fluctuations. An example was provided to demonstrate the use of simulation in the economic analysis of management options. In the example used, it appeared that an annual egg collection management program was not justifiable on a strictly economic basis.

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APPENDIX

Computer Program Used for Simulations

```
      PROGRAM GATRAID(INPUT,OUTPUT,TAPE60=INPUT,TAPE61=OUTPUT)
      REAL NESTEFF,NESTFLD,NATURAL(21,2),KILL
      INTEGER TEMP
      DIMENSION AGEINIT(21,2),HUNTING(14),REPROD(14),FLDLOSS(6),WATER(12
     1),DUMMY(21,2),SEX(2),WLEVEL(12,2),HARNUM(14),TOTSIZE(14),SURHUNM(2
     21,2),DESS1(15),DESS2(13),DESS3(9)
      DIMENSION IHARNUM(14),IFT(9)
      COMMON SURNATM,SURHUNM,NESTEFF,REPRATE,NESTFLD,EGGS,NYR
      COMMON APREQ,CANN,CANNMUL,CANNAB,DESS
      COMMON AGEINIT,TEMP,HUNRATE,MONTH,HACHTOT,PRED
      DATA WLEVEL/1.0,1.1,5*0.,.6,.9,.8,.4,.8,.39,.36,5*0.,.17,.44,.28,.
     129,.28/
      DATA SEX/5RMALE ,7RFEMALE /
      DATA WATER/12*.5/
      DATA NO/1RN/
      DATA REPROD/.335,.345,.355,.365,.38,.405,.45,.5,.56,.6,.63,.645,.6
     155,.67/
      DATA FLDLOSS/.03,.055,.08,.295,.515,.725/
      DATA NATURAL/.011,.044,.031,5*.033,13*.043,.011,.044,.031,5*.033,
     113*.02/
      DATA HUNTING/5.93,13.68,14.34,12.99,9.14,6.36,4.64,2.49,.53,3.77,6
     1.87,10.30,7.03,1.93/
      DATA DESS1/.0,.001,.003,.005,.007,.009,.012,.016,.022,.030,.041,.0
     161,.088,.120,.135/
      DATA DESS2/.0,.001,.002,.003,.006,.011,.017,.027,.043,.064,.082,.0
     194,.102/
      DATA DESS3/.0,.001,.002,.003,.006,.013,.023,.033,.037/
      READ(60,900)NUMYRS,AGEINIT
      PRINT 951
      WRITE(61,950)((AGEINIT(I,J),J=1,2),I=1,21)
      READ(60,911) HUNRATE,IDIFF
  911 FORMAT(F5.2,I2)
      XX=3379.
      CALL RANSET(XX)
      TOTS1=0.0    $    TOTS2=0.0    $    IGRTOT=0
      DO 1000 NYR=1,NUMYRS
      MN=0
      EGGS=0.
      MONTH=0
C*************INPUTS TO SYSTEM ARE WATER, DESIRED HARVEST, FREEZE OPTION
C             FREEZE OPTION IS ONLY INPUT FOR WINTER MONTHS
    5 MONTH=MONTH+1
      HUNSURV=1.0
      TOTAL=0.
      DO 1500 I=1,21
      TOTAL=TOTAL+AGEINIT(I,1)
 1500 TOTAL=TOTAL+AGEINIT(I,2)
      IF(MONTH.EQ.3)GO TO 10
      MN=MN+1
      WATER(MN)=FXLEVEL(WLEVEL,MN)
      IF(MONTH.NE.1)GO TO 9
      IF(HUNRATE.EQ.0)GO TO 9
      REPFEM=0.0
      HARFEM=0.0
      HARMAL=0.0
      HARTOT=0.
      DO 1700   I=9,21
 1700 REPFEM=REPFEM+AGEINIT(I,2)
      DO 1501 I=4,21
      HARMAL=HARMAL+AGEINIT(I,1)
      HARFEM=HARFEM+AGEINIT(I,2)
 1501 HARTOT=HARMAL+HARFEM
      WRITE(61,903)HARTOT
  903 FORMAT(2X,*TOT HARVESTABLE = *,F10.0)
      WRITE(61,1750) HARFEM
 1750 FORMAT(*+*,35X,*TOT HARVESTABLE FEMS =*,F10.0)
      WRITE(61,1751) REPFEM
 1751 FORMAT(*+*,75X,*TOT REPRODUCTIVE FEMS =*,F10.0)
      HARTOT=.01*HUNRATE*HARTOT
      WRITE(61,904)HARTOT
  904 FORMAT(2X,*AFTER PERC TAKEN *,F10.0)
      TOTSIZE(1)=AGEINIT(4,1)
      TOTSIZE(2)=AGEINIT(5,1)+AGEINIT(6,1)
      TOTSIZE(3)=AGEINIT(7,1)
      TOTSIZE(4)=AGEINIT(8,1)
      J=9
      DO 1503 I=5,8
      TOTSIZE(I)=AGEINIT(J,1)+AGEINIT(J+1,1)
```

(Continued)

Computer Program Used for Simulations (continued)

```
1503 J=J+2
     TOTSIZE(9)=AGEINIT(17,1)+AGEINIT(18,1)+AGEINIT(19,1)+AGEINIT(20,1
    1+AGEINIT(21,1)
     TOTSIZE(10)=AGEINIT(4,2)+AGEINIT(5,2)
     TOTSIZE(11)=AGEINIT(6,2)+AGEINIT(7,2)+AGEINIT(8,2)
     TOTSIZE(12)=AGEINIT(9,2)+AGEINIT(10,2)+AGEINIT(11,2)
     TOTSIZE(13)=AGEINIT(12,2)+AGEINIT(13,2)+AGEINIT(14,2)
     TOTSIZE(14)=0.
     DO 1504 I=15,21
1504 TOTSIZE(14)=TOTSIZE(14)+AGEINIT(I,2)
     WRITE(61,954)TOTSIZE
 954 FORMAT(2X,*TOTSIZE*,2(/,7F9.0))
     IF(IDIFF.EQ.1)  GO TO 1800
     TOTMALH=.70*HARTOT
     TOTFEMH=.30*HARTOT
     RATEMAL=TOTMALH/HARMAL
     RATEFEM=TOTFEMH/HARFEM
     DO 1810  I=1,9
1810 HARNUM(I)=RATEMAL*TOTSIZE(I)
     DO 1820  I=10,14
1820 HARNUM(I)=RATEFEM*TOTSIZE(I)
     GO TO 1850
1800 DO 1502  I=1,14
1502 HARNUM(I)=.01*HUNTING(I)*HARTOT
1850 DO 960  I=1,14
 960 IF(HARNUM(I).GT.TOTSIZE(I))  HARNUM(I)=TOTSIZE(I)
     WRITE(61,955)HARNUM
 955 FORMAT(2X,*HARNUM*,2(/,7F9.0))
     DO 1840  I=1,14
1840 IHARNUM(I)=HARNUM(I) + .5
     DO 1841  I=1,9
1841 IFT(I)=0
     DO 1843  I=1,9
1843 IFT(I)=IHARNUM(I)*(3+I)
     DO 1845  I=1,5
1845 IFT(I)=IFT(I)+(IHARNUM(I+9)*(3+I))
     WRITE(61,998) IFT
 998 FORMAT(*  IFT*,9I6)
     ITOTFT=0
     DO 1855  I=1,9
1855 ITOTFT=ITOTFT+IFT(I)
     IGRTOT=IGRTOT+ ITOTFT
     SCHED2=0.0      $     SCHED1=0.0
     SCHED2=7.5*IFT(1)
     DO 1860  I=2,9
1860 SCHED2=SCHED2+(IFT(I)*12.0)
     DO 1865  I=1,3
1865 SCHED1=SCHED1+(IFT(I)*14.0)
     DO 1869  I=4,5
1869 SCHED1=SCHED1+(IFT(I)*15.0)
     DO 1870  I=6,9
1870 SCHED1=SCHED1+(IFT(I)*16.0)
     TOTS1=TOTS1+SCHED1
     TOTS2=TOTS2+SCHED2
     DO 1511  I=1,14
     IF(TOTSIZE(I).NE.0.)GO TO 1511
     TOTSIZE(I)=1.
     HARNUM(I)=1.
1511 CONTINUE
     DO 1505 I=1,3
     SURHUNM(I,1)=1.
1505 SURHUNM(I,2)=1.
     SURHUNM(4,1)=(TOTSIZE(1)-HARNUM(1))/TOTSIZE(1)
     SURHUNM(5,1)=(TOTSIZE(2)-HARNUM(2))/TOTSIZE(2)
     SURHUNM(6,1)=SURHUNM(5,1)
     SURHUNM(7,1)=(TOTSIZE(3)-HARNUM(3))/TOTSIZE(3)
     SURHUNM(8,1)=(TOTSIZE(4)-HARNUM(4))/TOTSIZE(4)
     J=4
     DO 1506 I=9,15,2
     J=J+1
     SURHUNM(I,1)=(TOTSIZE(J)-HARNUM(J))/TOTSIZE(J)
1506 SURHUNM(I+1,1)=SURHUNM(I,1)
     DO 1507 I=17,21
1507 SURHUNM(I,1)=(TOTSIZE(9)-HARNUM(9))/TOTSIZE(9)
     SURHUNM(4,2)=(TOTSIZE(10)-HARNUM(10))/TOTSIZE(10)
     SURHUNM(5,2)=SURHUNM(4,2)
     J=11
     DO 1508 I=6,12,3
     SURHUNM(I,2)=(TOTSIZE(J)-HARNUM(J))/TOTSIZE(J)
     SURHUNM(I+1,2)=SURHUNM(I+2,2)=SURHUNM(I,2)
1508 J=J+1
     DO 1509 I=15,21
```

(Continued)

Computer Program Used for Simulations (continued)

```
1509 SURHUNM(I,2)=(TOTSIZE(14)-HARNUM(14))/TOTSIZE(14)
     DO 1510 I=4,21
     IF(SURHUNM(I,1).LT.0.)SURHUNM(I,1)=0.
     IF(SURHUNM(I,2).LT.0.)SURHUNM(I,2)=0.
1510 CONTINUE
     WRITE(61,953)SURHUNM
 953 FORMAT(2X,*HUNTING SURV RATES*,2(/,5X,21F5.3))
     WRITE(61,1880) ITOTFT,SCHED1,SCHED2
1880 FORMAT(*  TOTAL FT HARVESTED=*,I12,5X,*SCHED1 YIELD = $*,F15.2,5X,
    1*SCHED2 YIELD = $*,F15.2)
     IF(NUMYRS-NYR) 1898,1881,1898
1881 WRITE(61,1882) IGRTOT,TOTS1,TOTS2
1882 FORMAT(*  GRAND TOTAL FT=*,I12,* GRAND TOTAL SCHED1 =*,F15.2,* GRA
    1ND TOTAL SCHED2 =*,F15.2)
1898 CONTINUE
    9 CANNMUL=-1.46*WATER(MN)+1.73
      IF(WATER(MN).GE.1.01)CANNMUL=.25
      GO TO 15
   10 TEMP=1RN
      T=RANF(0)
      IF(T.LE..1)TEMP=1RY
      MN=7
      MONTH=7
C*************THIS SEGMENT COMPUTES PREDATION AND DESICCATION RATES TO BE
                ADDED TO NATURAL MORTALITY RATES GIVING TOTAL SURVIVORSHIP
                RATES FOR EACH AGE AND SEX CLASS
   15 DO 1200 ISEX=1,2
      DO 1300 ICLASS=1,21
      APRED=0.
      CANN=0.
      DESS=0.
      IF(MONTH.NE.7)GO TO 16
      IF(TEMP.EQ.NO)GO TO 1302
      SURNATM=.95
      GO TO 55
   16 IF(ICLASS.NE.1)GO TO 20
      CANN=.00000021*TOTAL-.0071
      IF(TOTAL.LE.38600.)CANN=.001
      IF(WATER(MN).GT.3.46)GO TO 25
      APRED=-.0236*WATER(MN)+.1318
      IF(WATER(MN).GT.-.8) GO TO 200
      IF(WATER(MN).LT.-2.2) WATER(MN)=-2.2
      I=10.*ABS(WATER(MN))-7.
      DESS=DESS1(I)
      GO TO 201
  200 DESS=0.0
  201 CONTINUE
      GO TO 30
   25 APRED=.05
      GO TO 30
   20 IF(ICLASS.NE.2)GO TO 35
      CANN=.00000016*TOTAL-.0055
      IF(TOTAL.LE.40600.)CANN=.001
      IF(WATER(MN).GT..91)GO TO 40
      APRED=-.024*WATER(MN)+.032
      IF(WATER(MN).GT.-1.0) GO TO 210
      IF(WATER(MN).LT.-2.2) WATER(MN)=-2.2
      I=10.*ABS(WATER(MN))-9.
      DESS=DESS2(I)
      GO TO 211
  210 DESS=0.0
  211 CONTINUE
      GO TO 30
   40 APRED=.01
      GO TO 30
   35 IF(ICLASS.NE.3)GO TO 44
      CANN=.00000005*TOTAL-.0016
      IF(TOTAL.LE.52000.)CANN=.001
   44 IF(ICLASS.GT.2.AND.ISEX.EQ.2.OR.ICLASS.GT.2.AND.ICLASS.LT.7.AND.IS
     1EX.EQ.1)GO TO 45
      GO TO 30
   45 IF(WATER(MN).GT.-1.4) GO TO 220
      IF(WATER(MN).LT.-2.2) WATER(MN)=-2.2
      I=10.*ABS(WATER(MN))-13.
      DESS=DESS3(I)
      GO TO 221
  220 DESS=0.0
  221 CONTINUE
C*************APPLY SURVIVORSHIP DUE TO HUNTING DURING SEPTEMBER
   30 IF(MONTH.NE.1)GO TO 31
      IF(HUNRATE.EQ.0)GO TO 31
      HUNSURV=SURHUNM(ICLASS,ISEX)
   31 CANNAB=CANNMUL*CANN
      SURNATM=1-(APRED+CANNAB+DESS+NATURAL(ICLASS,ISEX))
```

(Continued)

Computer Program Used for Simulations (continued)

```
C*************UPDATE AGE STRUCTURE
   55 AGEINIT(ICLASS,ISEX)=AGEINIT(ICLASS,ISEX)*SURNATM*HUNSURV
      IF(ISEX.EQ.2.AND.MONTH.EQ.10.AND.ICLASS.GT.8)GO TO 60
      GO TO 1301
C*************THIS SEGMENT COMPUTES PERCENTAGE OF FEMALES WHICH NEST AND
C                 TOTAL EGGS LAID
   60 AVG=(WATER(9)+WATER(10))/2.
      IF(AVG.LT..05)AVG=0.
      IF(AVG.GE..65)AVG=.67
      I=20.*AVG+1.
      NESTEFF=REPROD(I)
      REPRATE=NESTEFF*AGEINIT(ICLASS,ISEX)
      EGGS=EGGS+REPRATE*38.9
 1301 CALL SBPRINT(-1,WATER,ISEX,ICLASS)
 1300 CONTINUE
 1200 CONTINUE
 1302 CONTINUE
      IF(MONTH.NE.12)GO TO 5
      I=10
C*************THIS SEGMENT COMPUTES PERCENTAGE OF EGGS LOST DUE TO FLOODI
      IF(WATER(10)-WATER(11))65,70,70
   65 IF(WATER(11).LT.WATER(12))GO TO 75
      I=11
      GO TO 80
   70 IF(WATER(10)-WATER(12))75,80,80
   75 I=12
   80 IF(WATER(I).LT..9)GO TO 85
      IF(WATER(I).GE.1.5.AND.WATER(I).LT.4.)GO TO 90
      IF(WATER(I).GE.4.)GO TO 95
      GO TO 100
   85 NESTFLD=0.
      GO TO 105
   90 NESTFLD=.933
      GO TO 105
   95 NESTFLD=1.
      GO TO 105
  100 J=10.*WATER(I)-8.
      NESTFLD=FLDLOSS(J)
C*************THIS SEGMENT COMPUTES PERCENTAGE OF EGGS LOST DUE TO PREDAT
  105 PRED=.035
      IF(WATER(12).LT..2.OR.WATER(12).GT.1.2)GO TO 110
      IF(WATER(12).GE..2.AND.WATER(12).LE..8)GO TO 115
      PRED=-.825*WATER(12)+1.025
      GO TO 110
  115 PRED=.55*WATER(12)-.075
  110 HACHTOT=(EGGS*(1.-NESTFLD))*(1.-PRED)*.768
C*************MOVE ALL AGE CLASSES UP INTO NEXT YEAR CLASS
      DO 1400 I=1,20
      DUMMY(I+1,1)=AGEINIT(I,1)
 1400 DUMMY(I+1,2)=AGEINIT(I,2)
      DO 1401 I=2,21
      AGEINIT(I,1)=DUMMY(I,1)
 1401 AGEINIT(I,2)=DUMMY(I,2)
C*************COMPUTE NEW ZERO YEAR CLASS
      AGEINIT(1,1)=HACHTOT*.601
      AGEINIT(1,2)=HACHTOT*.399
      CALL SBPRINT(1,WATER,ISEX,ICLASS)
      TOTAL = 0.0
      DO 1910  J=1,2
      DO 1910  I=1,21
 1910 TOTAL=TOTAL+AGEINIT(I,J)
      IF(NYR.EQ.1)  OLDTOT=100000.
      IF(NYR.EQ.1)  TOTLAM=1.0
      XLAMBDA=TOTAL/OLDTOT
      TOTLAM=TOTLAM*XLAMBDA
      OLDTOT=TOTAL
      WRITE(61,1903) XLAMBDA
 1903 FORMAT(*+*,55X,*LAMBDA=*,F10.6)
      IF(NUMYRS-NYR) 1908,1904,1908
 1904 XNUMYRS=NUMYRS
      XMEAN=TOTLAM**(1./XNUMYRS)
      WRITE(61,1905) XMEAN
 1905 FORMAT(*+*,80X,*MEAN LAMBDA=*,F10.6)
 1908 CONTINUE
 1000 CONTINUE
  900 FORMAT(I2,3(/,14F5.0))
  901 FORMAT(F5.2)
  950 FORMAT(41X,*MALES*,10X,*FEMALES*,//,21(37X,F9.0,7X,F9.0,/))
  951 FORMAT(*0*,10X,*INITIAL AGE STRUCTURE*)
  952 FORMAT(10X,*NUMBER OF *,R7,*HARVESTED FROM *,I2,* AGE CLASS =*,F9.
     10)
      END
```

(Continued)

Computer Program Used for Simulations (continued)

```
      FUNCTION FXLEVEL(WLEVEL,MONTH)
      DIMENSION WLEVEL (12,2)
      SUM=0.
      DO 100 I=1,12
  100 SUM=SUM+RANF(0)
      FXLEVEL=(SUM-6.)*WLEVEL(MONTH,2)+WLEVEL(MONTH,1)
      RETURN
      END
      SUBROUTINE SBPRINT(JBUG,WATER,ISEX,ICLASS)
      REAL NESTEFF,NESTFLD
      INTEGER TEMP,YES
      DIMENSION MONTHS(12),WATER(12)
      DIMENSION SEX(2)
      COMMON SURNATM,SURHUNM(21,2),NESTEFF,REPRATE,NESTFLD,EGGS,NYR
      COMMON APRED,CANN,CANNMUL,CANNAB,DESS
      COMMON AGEINIT(21,2),TEMP,HUNRATE,MONTH,HACHTOT,PRED
      DATA SEX/5HMALE  ,7HFEMALE /
      DATA MONTHS/9HSEPTEMBER,7HOCTOBER,0,0,0,0,6HWINTER,5HAPRIL,3HMAY,4
     1HJUNE,4HJULY,6HAUGUST/
      DATA YES/1HY/
      IF(JBUG.LT.0)RETURN
      IF(JBUG)4,9,9
    4 IF(MONTH.EQ.1)GO TO 5
      RETURN
    5 WRITE(61,101)ISEX,ICLASS,MONTHS(MONTH)
      WRITE(61,100)CANNMUL,CANN,CANNAB,APRED,SURNATM,SURHUNM(ICLASS,ISEX
     1),DESS
      IF(MONTH.EQ.10.AND.ISEX.EQ.2.AND.ICLASS.GT.8)GO TO 11
      RETURN
   11 WRITE(61,108)NESTEFF,REPRATE,EGGS
      RETURN
    9 WRITE(61,113)NYR
      WRITE(61,102)MONTHS(MONTH)
      IF(MONTH.EQ.1)WRITE(61,103)HUNRATE
      IF(MONTH.EQ.7)GO TO 15
      WRITE(61,111)WATER(MONTH)
      GO TO 20
   15 IF(TEMP-YES)25,30,25
   25 PRINT 104
      GO TO 20
   30 PRINT 105
   20 IF(JBUG.NE.1)GO TO 32
      PERCN=100.*NESTEFF
      WRITE(61,112)PERCN,EGGS
      PERCN=100.*NESTFLD
      PERCP=100.*PRED
      WRITE(61,110)PERCN,PERCP
      WRITE(61,109)HACHTOT,AGEINIT(1,1),AGEINIT(1,2)
   35 PRINT 106
      DO 31 I=1,21
   31 WRITE(61,107)I,AGEINIT(I,1),AGEINIT(I,2)
   32 TOTAL=0.
      DO 1500 J=1,2
      SUM=0.
      DO 1501 I=1,21
 1501 SUM=SUM+AGEINIT(I,J)
      WRITE(61,902)SEX(J),SUM
 1500 TOTAL=TOTAL+SUM
      WRITE(61,903)TOTAL
      RETURN
  101 FORMAT(2X,*SEX =*,I2,2X,*CLASS =*,I3,A10)
  902 FORMAT(16X,R10,*POPULATION = *,F12.0)
  903 FORMAT(20X,*TOTAL POPULATION = *,F12.0)
  113 FORMAT(1X,10H**********,*YEAR *,I2)
  100 FORMAT(2X,*CANNMUL=*,F4.2,*CANN=*,F4.2,*CANNAB=*,F4.2,*APRED=*,F4.
     12,*SURNATM=*,F4.2,*SURHUNM=*,F4.2,1X,*DESS=*,F4.2)
  108 FORMAT(2X,*NESTEFF=*,F10.3,2X,*REPRATE=*,F10.3,2X,*EGGS= *,F10.3)
  102 FORMAT(*0*,10X,*END OF *,A10)
  103 FORMAT(20X,*HARVEST DESIRED IS *,F6.2,* PERCENT*)
  104 FORMAT(20X,*NO FREEZE DURING WINTER*)
  105 FORMAT(20X,*FREEZE APPLIED DURING WINTER*)
  106 FORMAT(*0*,30X,*NEW AGE STRUCTURE*,/,40X,*MALES*,10X,*FEMALES*)
  107 FORMAT(32X,I2,2X,F9.0,7X,F9.0)
  109 FORMAT(*0*,20X,*TOTAL HATCHINGS FOR YEAR = *,F12.0,1X,*CONSISTING
     1OF *,F12.0,1X,*MALES AND *,F12.0,1X,*FEMALES*)
  110 FORMAT(2X,*PERCENTAGE OF EGGS  LOST DUE TO FLOODING =*,F5.1,/,2X,*
     1PERCENTAGE OF EGGS  LOST DUE TO PREDATION =*,F5.1)
  111 FORMAT(12X,*AVERAGE WATER LEVEL FOR MONTH IS *,F5.2)
  112 FORMAT(2X,*PERCENTAGE OF FEMALES NESTING =*,F5.1,1X,*YIELDING*,F10
     1.0,1X,*EGGS*)
      END
```